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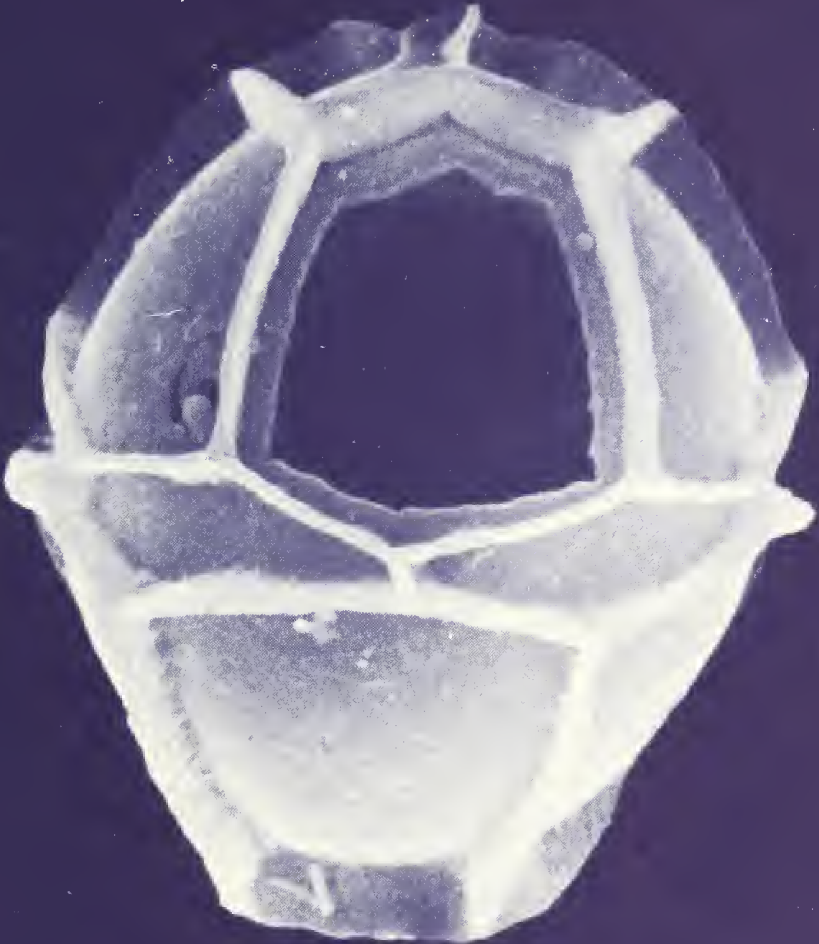

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Cover: The dinoflagellate cyst *Impagidinium patulum* (Wall) Stover and Evitt, from bottom sediments in the North Atlantic Ocean. British Geological Survey specimen M.P.K. 4234. × 2500.

ESTIMATING BIOMASS AND ENERGY FLOW OF MOLLUSCS IN PALAEO-COMMUNITIES

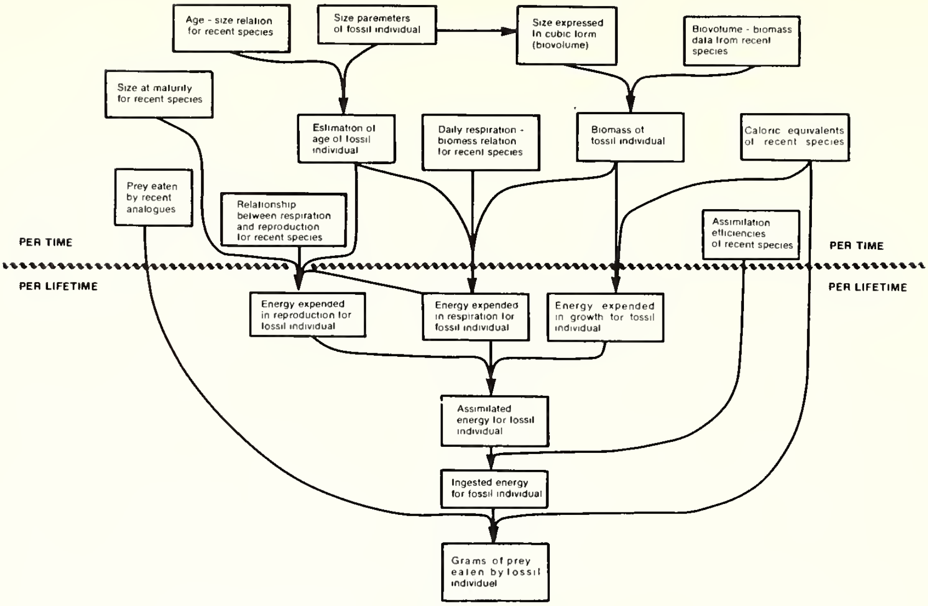
by E. N. POWELL *and* R. J. STANTON, JR.

ABSTRACT. The reconstruction and interpretation of palaeo-community structure has been based largely on the taxonomic composition and relative abundance of the perserved species. An expanded and more precise understanding of some aspects of the palaeo-community can be deduced from information on the biomass and energy flow of its preserved components. The procedural steps to calculate energy flow in a palaeo-community require as input the size-frequency distribution of each species' population, the size-age relationship for each species, and certain parameters of energy flow that have been measured for living organisms. These parameters are used to: (1) estimate biomass from size, (2) convert biomass into its caloric equivalent, (3) estimate respiration from biomass and age, (4) estimate the energy cost of reproduction from respiration and size at maturity, and (5) calculate total assimilated energy from (2), (3), and (4) above. The quantity of food consumed by an individual or population can also be estimated because ingestion can be estimated from assimilation. These estimates must be summed over the individual's life span rather than evaluated on a yearly time scale, as is normally done in ecologic studies. Therefore, calculations of energy flow may differ substantially from those elucidated in studies of recent communities. The method is used to determine the energy flow in populations of four gastropods and one bivalve from the Stone City Formation (Eocene) of east-central Texas. The relative importance of species differs considerably if assessed by their numerical abundance, their biomass, or the amount of food ingested by them over their lifetimes. For example, *Hesperiturris nodocarinatus*, the least abundant species numerically, ingested the most prey biomass.

A CHRONIC problem in ecologic and palaeoecologic research is to adequately interpret community structure and dynamics from data consisting only of species composition and numerical abundance. Numerical abundance, however, may over-emphasize the importance in the living community of opportunistic species or species with particularly successful larval sets because of low juvenile survivorship (Thorson 1966) and frequently occurring disturbances (Gray 1977; Woodin 1978) in the community. Such species also may dominate the numerical abundance of the death assemblage (Levinton 1970; Powell *et al.* 1984) and the resulting fossil assemblage, so that the actual importance of other species may not be evaluated accurately from abundance data during community reconstruction. Stanton *et al.* (1981) discussed this problem in relation to the trophic reconstruction of palaeo-communities. In that case, use of abundance data over-emphasized the importance of naticid gastropods in the community's trophic structure (Stanton and Nelson 1980) because most of the individuals were small and contributed little biomass to, and had little predatory impact on, the total community. Stanton *et al.* (1981) argued that analysis of trophic structure based on biomass should be more accurate than on abundance, but they were constrained by the absence of a good procedure for determining biomass from size.

Odum and Smalley (1959) pointed out that, although the use of numerical abundance tends to over-emphasize the importance of small organisms, biomass tends to over-emphasize the importance of large organisms. Thus, Odum and Smalley (1959), Steele (1976), and others argued that energy flow provides the best method for interpreting the trophic structure of communities. Stanton *et al.* (1981) suggested that this should be true for palaeo-community reconstructions as well, but pointed out the primary difference between estimations of energy flow in ecology and palaeoecology. That is, energy flow in ecology is normally measured on a per area per year basis whereas energy flow in palaeoecology must be evaluated for an individual's entire lifetime. The absence of conversion equations to predict energy flow from size-frequency data prevented Stanton *et al.* (1981) from further investigation of this subject.

[Palaeontology, Vol. 28, Part 1, 1985, pp. 1-34.]

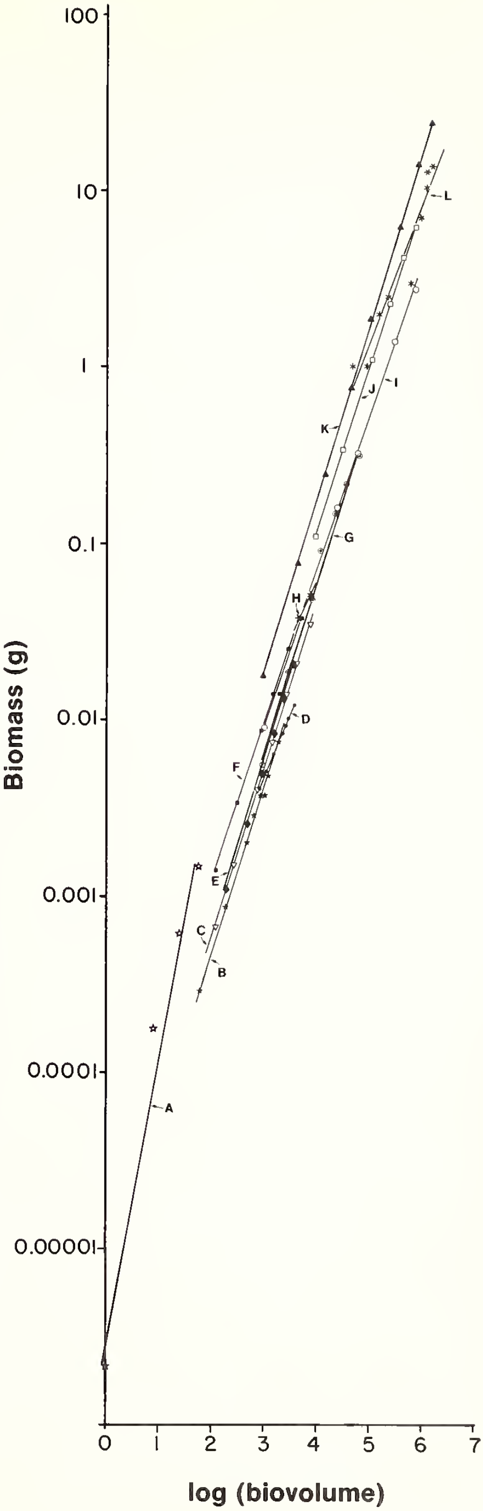

Age - size relation for recent species
Size paremeters of fossil individual
Size expressed in cubic form (biovolume)
Biovolume - biomass data from recent species
Size at maturity for recent species
Estimation of age of fossil individual
Daily respiration - biomass relation for recent species
Biomass of fossil individual
Caloric equivalents of recent species
Prey eaten by recent analogues
Relationship between respiration and reproduction for recent species
Assimilation efficiencies of recent species
PER TIME
PER TIME
PER LIFETIME
PER LIFETIME
Energy expended in reproduction for fossil individual
Energy expended in respiration for fossil individual
Energy expended in growth for fossil individual
Assimilated energy for fossil individual
Ingested energy for fossil individual
Grams of prey eaten by fossil individuel

TEXT-FIG. 1. Steps in determining energy flow.

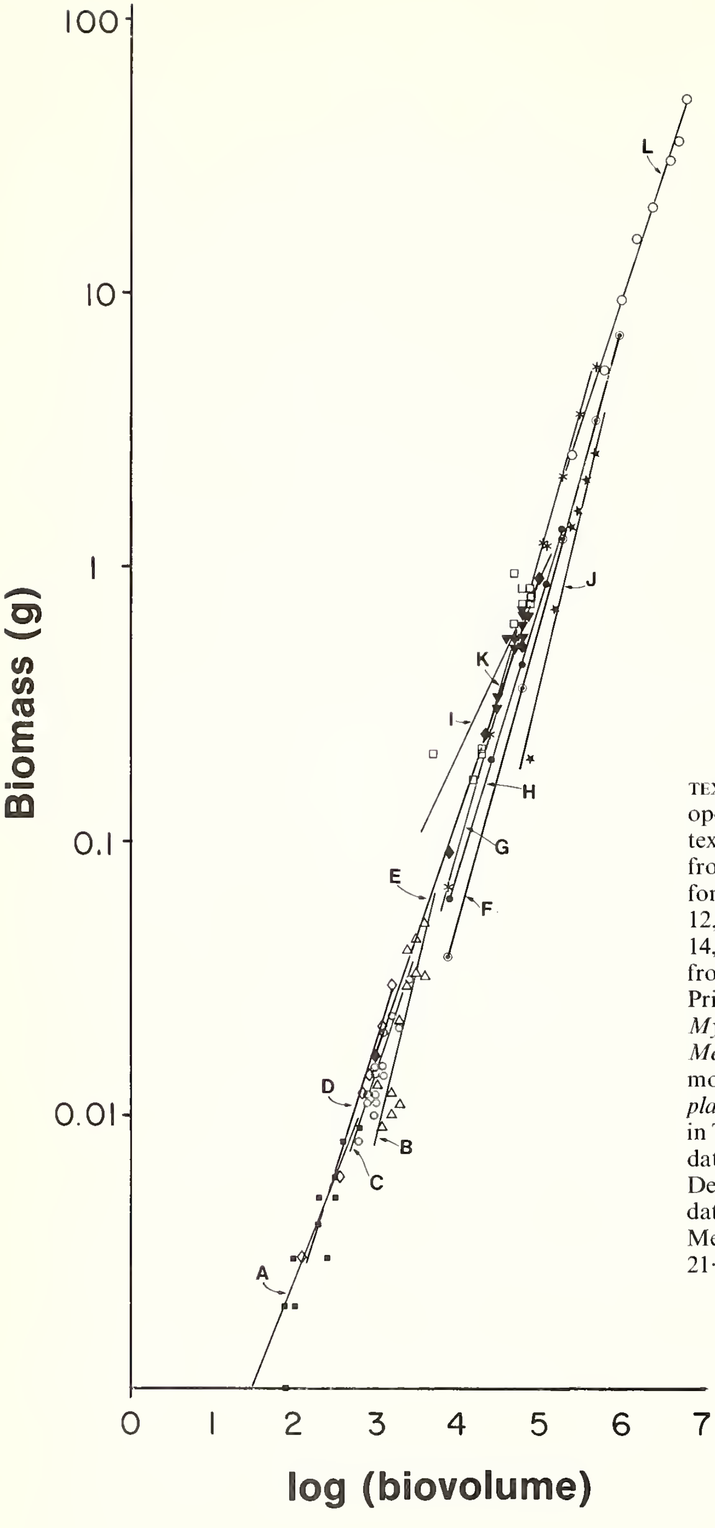
In this paper we present conversion equations for calculating biomass and energy flow from numerical abundance and size-frequency data, and discuss the assumptions behind these conversions. Similar approaches have been used for terrestrial vertebrates (Martin 1980; Scott 1982). To demonstrate the application of this method in palaeoecology, the parameters of energy flow will be evaluated for five of the species of Eocene molluscs discussed by Stanton *et al.* (1981) and Stanton and Nelson (1980). In deriving these equations, we have sought relatively simple procedures that require measurements of size commensurate with the quality of numerical abundance and size-frequency data normally available to palaeontologists. The data and equations deal specifically with molluscs. Although the method of conversion would be the same, different equations might be required for other phyla. Whenever possible we utilize one equation for molluscs as a whole or two equations, one for bivalves and one for gastropods. Although a higher degree of accuracy might be obtained, in some cases, by a series of equations for lower taxonomic levels, the data base available is not sufficiently large for this to be a viable alternative for many living taxa, and of course many extinct taxa have no recent analogues.

The steps in estimating biomass and energy flow are diagrammed in text-fig. 1. The biomass of a species' population in a community is the sum of the biomasses of all of the individuals in that population. It is determined, then, from (1) the number of individuals present, (2) the size-frequency distribution of the population, and (3) the relationship between size and biomass for each individual. In the following section we present simple equations for calculating biomass from shell dimensions for bivalves and gastropods. To do this, shell dimensions are converted by simple equations into operational biovolumes which subsequently can be converted to true biomass. The biovolumes are not true biovolumes as might be derived, for example, from displacement volume, but rather are simply shell dimensions transposed into a convenient cubic form.

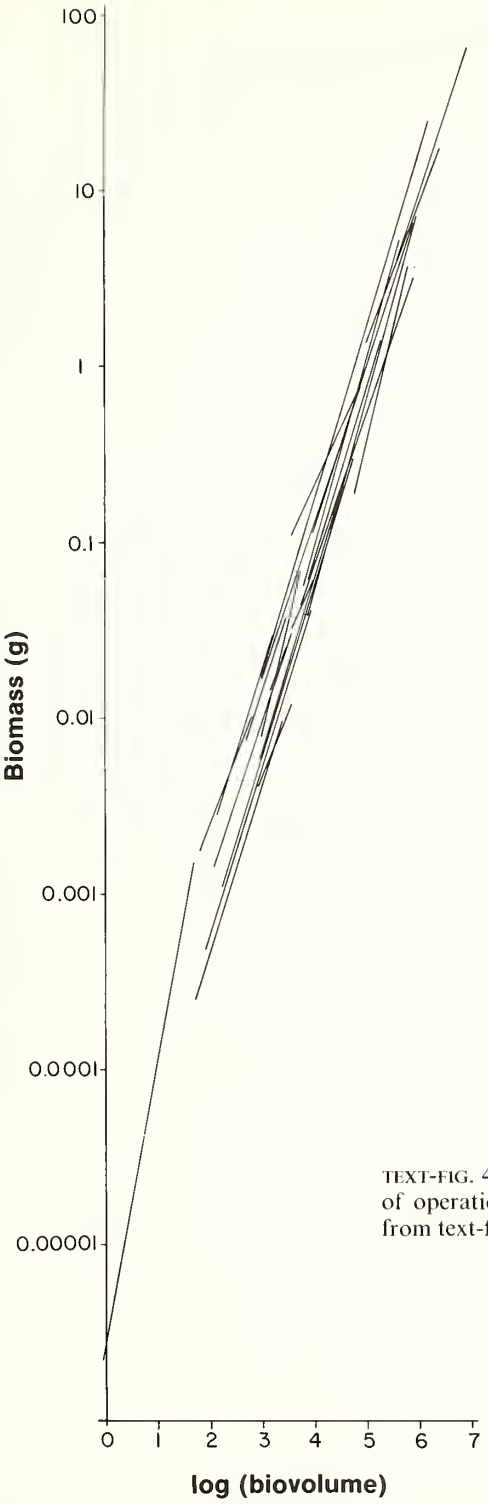
Assimilated energy is expended largely in growth, respiration, and reproduction. In the second section we present equations for the estimation of these parameters from the individual's biomass using relationships obtained from data on living molluscs. These relationships include a caloric equivalent of biomass, the daily respiration rate at a given biomass, and the amount of energy expended in reproduction relative to that expended in respiration. Energy expended in growth,



TEXT-FIG. 2. Regression lines of bivalve biomass versus log of operational biovolume (= cube of the maximum length). Additional bivalves are plotted in text-fig. 3. Data points indicate those data used from the individual data sets to calculate the final biomass–biovolume regression. In literature sources where regression lines were given but original data points were not, data points have been generated from these length–biomass regressions, and span the length range of the original data set. Information about the data sources is listed in the following order: taxon, reference, number of data points, comments, biomass measure (DW, dry weight; AFDW, ash-free dry weight; FDDW, freeze-dried dry weight; form, formalin perserved specimens; EtOH, alcohol preserved specimens; no designation, fresh or frozen specimens). A (☆): *Gemma gemma*, Green and Hobson (1970), 4, average length–DW regression for shelled animals and AFDW = 8·9% DW, AFDW. B (▼): *Abra nitida*, Wikander (1980), 7, from regression equation, AFDW. C (▽): *A. longicallus*, Wikander (1980), see B. D (●): *Spisula elliptica*, Ford (1925), 7, from Table III, DW EtOH. E (◆): *Nuculana minuta*, Ansell *et al.* (1978), 6, total wt–L^3 regressions and DW = 4·88% total wt., DW. F (■): *Macoma balthica*, Bachelet (1980), 5, average of monthly regression equations, AFDW after decalcification. G (⦿): *Tagelus divisus*, Fraser (1967), 7, average of monthly regressions (for L > 2·5 cm) and single regression equation (for L < 2·5 cm) from Table 1, DW. H (✱): *Cardium echinatum*, Ford (1925), 2, DW EtOH. I (o): *Mytilus californianus*, Fox and Coe (1943), 8, from Table 1, DW. J (□): *Mya arenaria*, Feder and Paul (1974), 7, from regression equation, DW. K (▲): *Tresus capax*, Breed-Willeke and Hancock (1980), 8, from Table 3, DW. L (✱): *Arctica islandica*, Ropes (1971) 9, from fig. 1, FDDW.



TEXT-FIG. 3. Regression lines of bivalve biomass versus log of operational biovolume (= cube of maximum length). See text-fig. 2 for format. A (■): unidentified venerid collected from Kahn Creek, Dubai, U.A.E., our data, 11, AFDW form. B (▵): *Macoma balthica*, Beukema and DeBruin (1977), 12, from fig. 1, AFDW. C (◎): *Mulinia lateralis*, our data, 14, AFDW. D (◇): *Tellina martinicensis*, Penzias (1969), 6, from fig. 5, DW. E (◆): *Cerastoderma edule*, Warwick and Price (1975), 5, from regression equation, AFDW. F (◉): *Mya arenaria*, Warwick and Price (1975), see E. G (✱): *Mercenaria mercenaria*, Hibbert (1977*a*), 7, average of monthly regressions in Table 2, AFDW. H (●): *Scrobicularia plana*, Hughes (1970), 5, from average of monthly regressions in Table 1, DW. I (□): *Anadara* sp., from Dubai, U.A.E., our data, 13, AFDW form. J (★): *Tagelus plebeius*, Holland and Dean (1977), 6, from fig. 4, DW. K (▼): *M. mercenaria*, our data, 10, AFDW. L (○): *Spisula solidissima*, Barker and Merrill (1967), 8, from fig. 3 using mean percentage solids of 21·4 to convert wet wt. to FDDW, FDDW.



TEXT-FIG. 4. Regression lines for bivalve biomass versus log of operational biovolume. Regression lines are combined from text-figs. 2 and 3.

respiration, and reproduction, however, are expressed in terms of the total energy used over the individual's life span because energy flow occurs throughout the individual's life and, for a fossil, the individual has completed its life span. For this reason, the age at sexual maturity, age at death, and a relationship between size and age also must be known. Then, by utilizing assimilation efficiencies of recent molluscs, we predict the quantity of food ingested over the individual's life span. In each step we list the sources of inaccuracy present in the calculation and, where possible, test the degree of accuracy by comparing independently published data with those predicted by our equations. In the last section we apply our results to the Stone City (Eocene) fauna in order to demonstrate the differences in interpretation that result from the use of biomass and energy flow rather than numerical abundance for trophic reconstruction of palaeo-communities.

BIOMASS

Biomass in a bivalve or gastropod is correlated with the volume of the body cavity within the shell. Thus, one could determine biomass for fossils from the relationships of size to biovolume, and biovolume to biomass for living molluscs. True biovolume is tedious to measure, however, so we chose, instead, to use an operational measurement of biovolume based on the conversion of easily measured shell parameters into cubic form. Regressions of true biovolume, obtained by filling shells with paraffin under vacuum, dissolving the shell in 10% HCl and weighing the paraffin, with operational biovolume for three species, *Thais haemastoma*, *Polinices duplicatus*, and *Littorina ziczac*, all had correlation coefficients above 0·95, proving the efficacy of this method. For bivalves, biomass is plotted in text-figs. 2–4 against the cube of the maximum (anterior–posterior) length, as suggested by Golightly and Kosinski (1981). For gastropods, the operational biovolume is the equation for the volume of a cone computed from maximum length and width, except for the limpet, in which case a formula for a general prismatoid is used. Gastropod biomass is plotted against operational biovolume in text-figs. 5–7. The equations for biomass in terms of operational biovolume derived from the regression lines for these plots are in the form:

$$\log_{10} B = m_B \log_{10} V + b_B \qquad (1)$$

where V is operational biovolume in mm^3 and B is biomass in grams. They are:

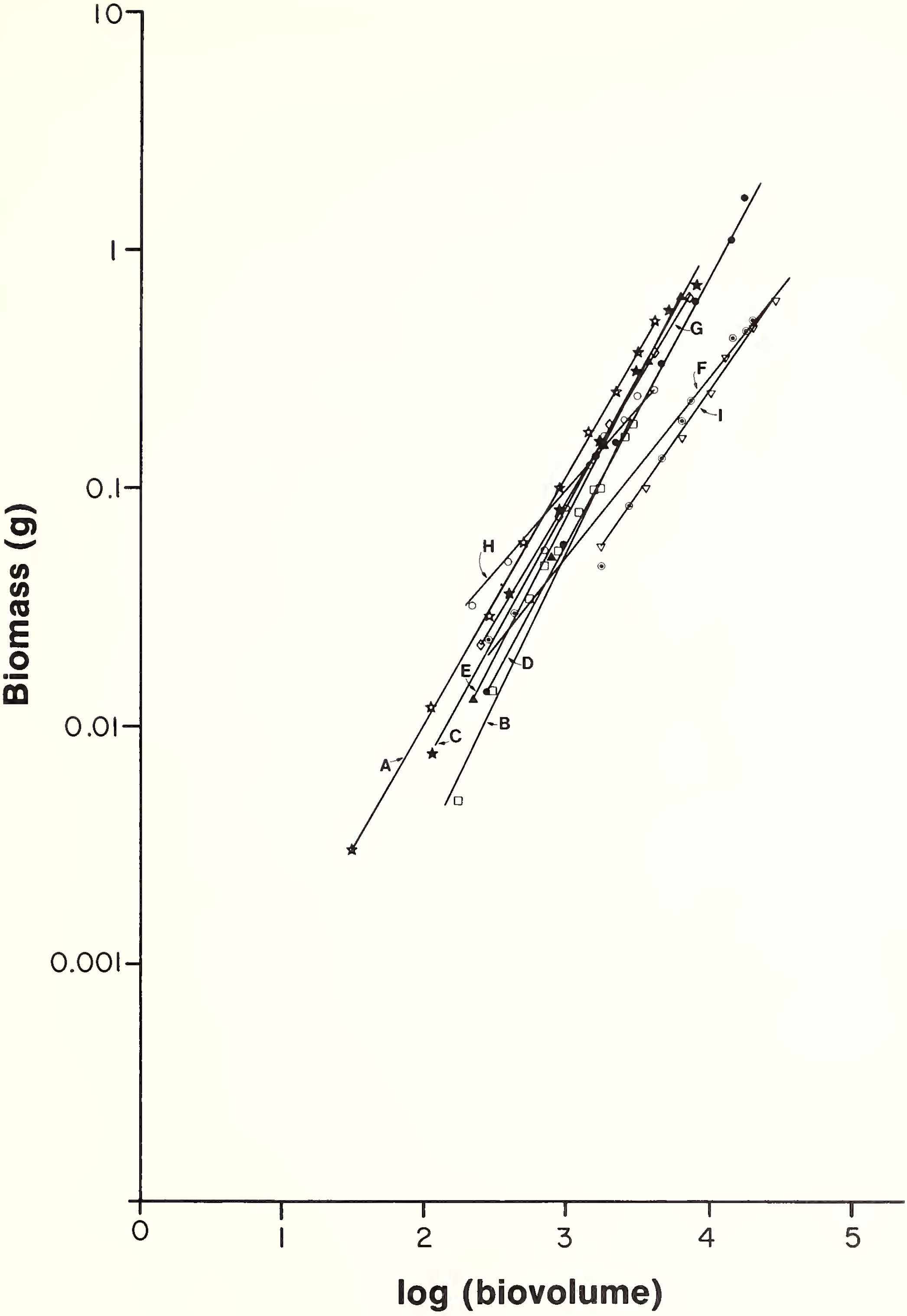
for bivalves,

$$\log B = (0{\cdot}9576 \pm 0{\cdot}0004) \log V + (-4{\cdot}8939 \pm 0{\cdot}0065) \qquad r = 0{\cdot}98 \quad (1a)$$

for gastropods,

$$\log B = (0{\cdot}7708 \pm 0{\cdot}0019) \log V + (-3{\cdot}2421 \pm 0{\cdot}0152) \qquad r = 0{\cdot}88 \quad (1b)$$

TEXT-FIG. 5 (*opposite*). Regression lines of gastropod biomass versus log of operational biovolume. Additional gastropod data are plotted in text-fig. 6. Except where noted, operational biovolume was computed from $V = \frac{1}{3} \cdot \pi \cdot (W/2)^2 \cdot L$, where W = maximum whorl width, and L = maximum apex–abapical tip length. W/L is estimated from cited figures in Abbott (1974) except where noted. See text-fig. 2 for format used below. A (☆): *Diloma novaezelandiae*, Logan (1976), 9, DW-shell diameter regression and $W/L = 0{\cdot}97$ from figs. 8–9 in Cernohorsky (1974), DW. B (□): *Thais emarginata*, Palmer (1982), 10, L–body wt. from Table 2 and AFDW–body wt. regression Table 1 with $W/L = 0{\cdot}77$ from fig. 1909, AFDW. C (★): *Fissurella barbadensis*, Hughes (1971*a*), 7, body wt.–shell length regression equation, calculation of biovolume used the equation for a general prismatoid $V = \frac{1}{6}L(B_1 + 4M + B_2)$ where L is dorsal-ventral shell height, B_1, the area of a rectangle approximating the ventral base of the shell, M, the area of a rectangle at $L/2$, B_2, the area of a rectangle at the apex (assumed $B_2 = 0$), relationship of B_1, M, L to shell length from Abbott (1974), fig. 130, DW. D (●): *Nerita peloronta*, Hughes (1974*b*), 7, regression equation, assumed $W/L = 1{\cdot}05$ from fig. 519, DW. E (▼): *N. tesselata*, Hughes (1971*b*), 5, see D, W/L = 0·94 from fig. 521. F (⊙): *T. lamellosa*, Palmer (1982), 10, see B, assumed $W/L = 0{\cdot}63$ from fig. 1905. G (◇): *N. versicolor*, Hughes (1971*b*), see E, assumed $W/L = 1{\cdot}0$ from fig. 520. H (○): *T. canaliculata*, Palmer (1982), see B, assumed $W/L = 0{\cdot}60$ from fig. 1904. I (▽): *Polinices duplicatus*, Edwards, D. C. and Huebner (1977), 7, from AFDW–W regression and W–L regression, AFDW.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0.01
0.001
Biomass (g)
0
1
2
3
4
5
log (biovolume)
A
B
C
D
E
F
G
H
I

Text-figs. 4 and 7 contain all the individual regression lines for the bivalve and gastropod data respectively. The same lines are presented in text-figs. 2 and 3 (bivalves), and 5 and 6 (gastropods) at a larger scale so they can be examined in more detail. Some of the data points in text-figs. 2 and 3, and 5 and 6 were generated from the published regression lines if original data points were not given. Although these generated points cover the size range of individuals used by the original authors, the variability of our data is certainly less than that of the original data set. Therefore confidence limits and correlation coefficients are conditional. Data subsets used in text-figs. 2–7 are of similar size so that no one subset would be inordinately important in the regression.

The variability around the regression lines is smaller than one might anticipate, considering the wide array of shapes and sizes of bivalve and gastropod species included in the regressions. The gastropods used, for example, range in shape from naticids to muricids and columbellids; bivalves include cardiids, tellinids, and razor clams (*Tagelus*). Although a few taxa, such as the razor clam *Ensis* and some gastropods such as *Conus* or *Crepidula* may require different equations for operational biovolume (data for the limpet *Fissurella*, for example, fit the biomass curve when the equation for a prismatoid was used), these equations appear to be useful for the great majority of bivalves and gastropods.

The scatter of data points around the two main regression lines may be due in part to any of the following: (1) Seasonal reproductive cycles that can cause significant variability in biomass among individuals of the same species at a single location (see references in text-figs. 2–7). (2) Regional differences in shape and growth result in differences within a species in the biovolume to biomass relationship (Hamai 1938; Clark 1976; Eisma *et al.* 1976). (3) Differences in the methods used for measuring biomass; some are less accurate than others (Mills *et al.* 1982). (4) The equations for operational biovolume require measurements readily made from most fossils. More complex equations (Raup and Graus 1972; Kohn and Riggs 1975; Harasewych 1981) might estimate biovolume more accurately but would require measurements often not easily obtainable from fossils. Probably, the primary source of error in determining biomass is intraspecific variability. This will be difficult to eliminate. The range of variability among the gastropod regression lines is bracketed by regression lines for two samples of the same species, *P. duplicatus*, and by regression lines for two species of the same genus *Thais* and *Thais* (*Nucella*), for example. Thus, we use two general equations, 1a and 1b, to generate biomass rather than a larger number of equations derived from data sets each restricted to taxa of lower taxonomic level.

ENERGY FLOW

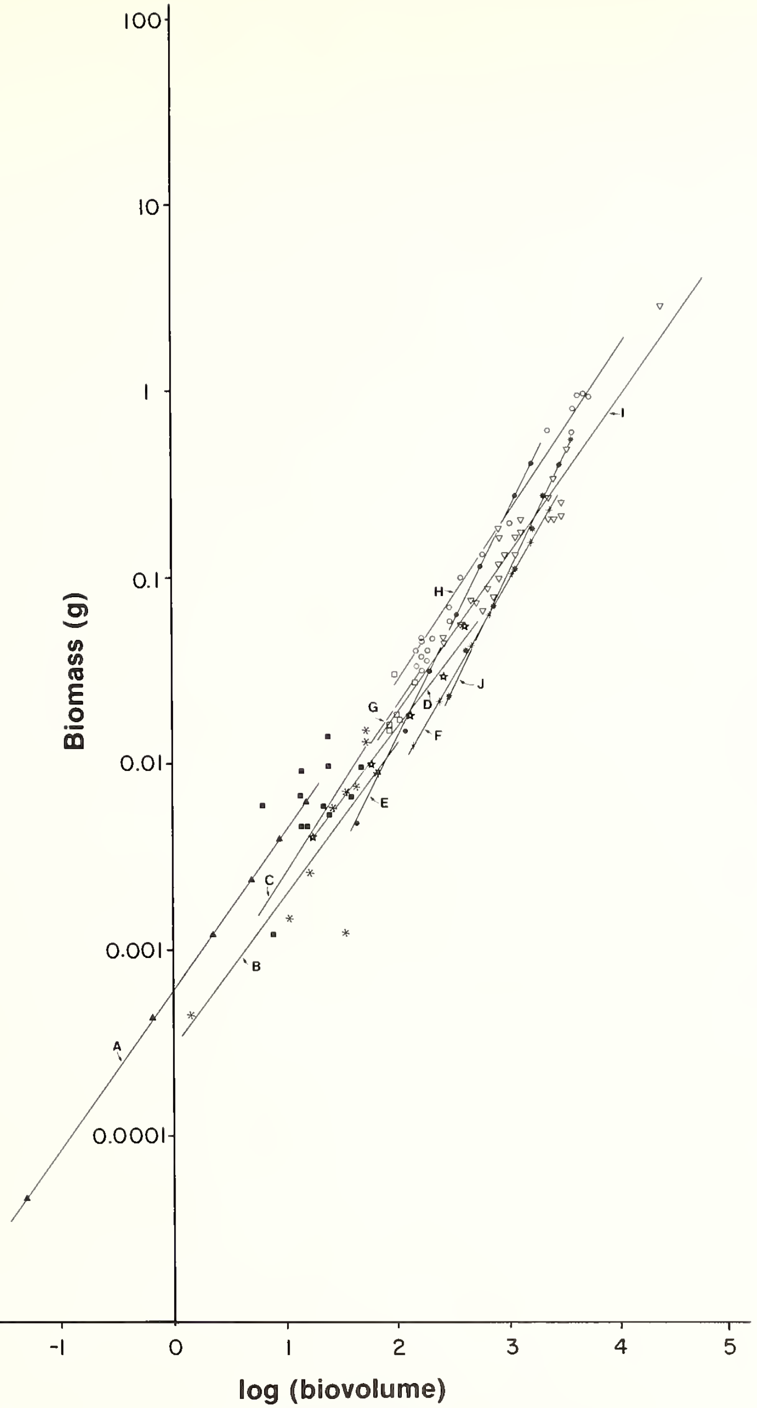
Assimilated energy (A) is expended largely in growth (P_g), respiration (R), and reproduction (P_r). The energy costs of excretion and secretion are assumed to be small by most referenced workers and will be assumed to be negligible here. Energy flow is calculated in ecology in terms of $\mathrm{cal \cdot m^{-2} \cdot yr^{-1}}$. Energy flow can only be calculated in palaeoecology, however, for an organism's life span ($\mathrm{cal \cdot lifetime^{-1}}$) because the data base consists of dead shells, which obviously have completed their life spans. Each of these energy uses—growth, respiration, and reproduction—varies with the size and age of the organism. Therefore, in order to estimate the amount of energy used in an organism's lifetime, both an individual's age and size must be known.

Estimation of age

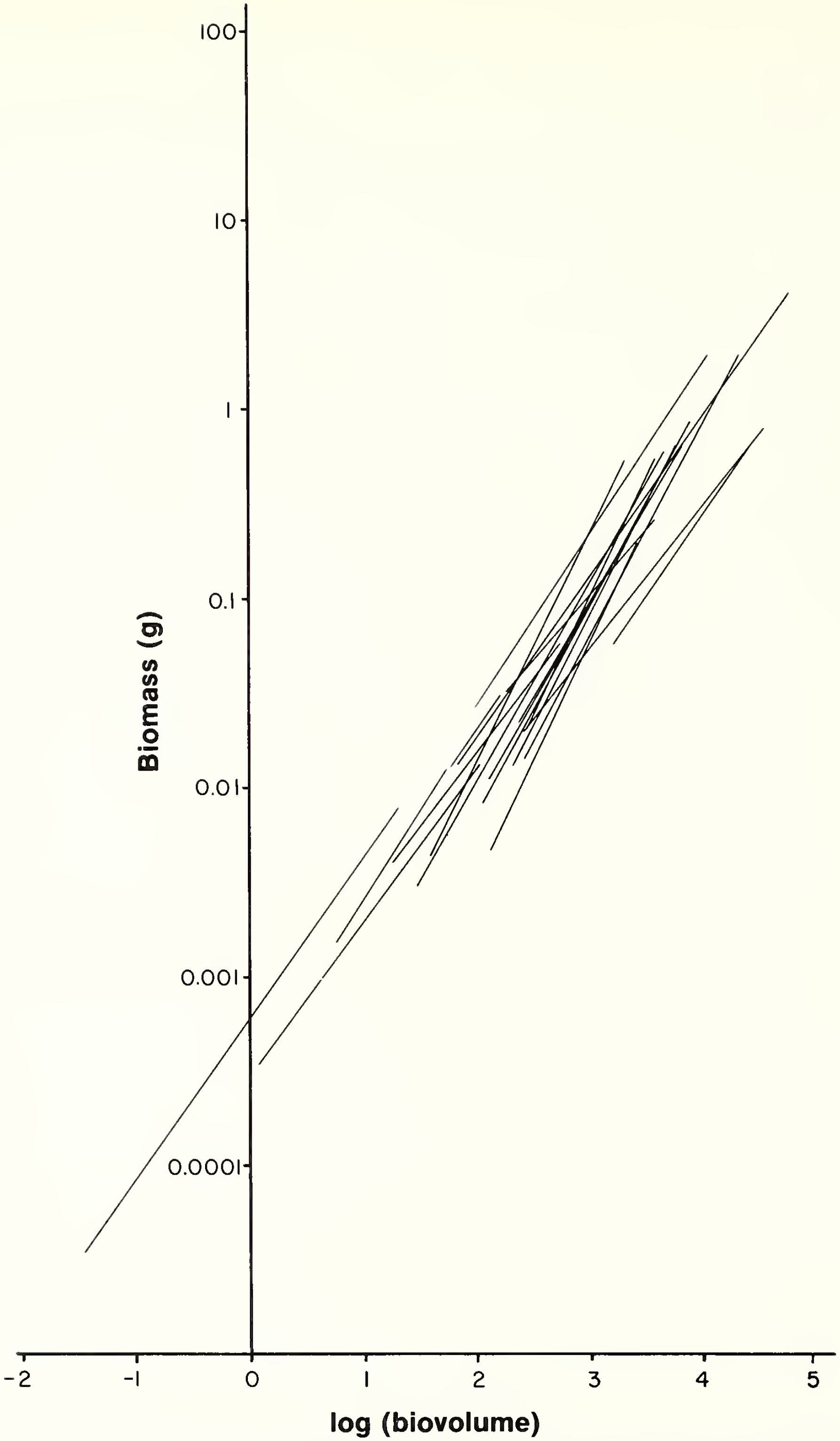
An estimate of age can be obtained using the general logarithmic relationship between size and age (Levinton and Bambach 1970).

$$S = s_T \log_{10}(T+1) \tag{2}$$

where S is a linear measurement of size; s_T, a species-specific constant, and T, the elapsed time since birth, or age at death. Ideally age would be determined more specifically for each individual by some means such as daily or annual shell banding (Tevesz 1972; Jones 1980), but this may not be practical



TEXT-FIG. 6. Regression lines of gastropod biomass versus log of operational biovolume. See text-figs. 2 and 5 for format. A (▼): *Potamopyrgus jenkinsi*, Simpson (1978), 6, average of all L-organic carbon regressions Table 1 and organic carbon-DW regressions Table 2, assumed $W/L = 0{\cdot}54$ from pl. 10.3, McMillan (1968), DW. B (✻): *Anachis avara*, our data, 11, W/L measured, AFDW. C (■): *Littorina ziczac*, our data, 13, W/L measured, AFDW. D (☆): *L. planaxis*, North (1954), 5, from fig. 7, assumed $W/L = 0{\cdot}74$ from fig. 553, DW. E (●): *Tegula funebralis*, Paine (1971), 8, from regression equation for total of 1965 and 1966 Table 2, assumed $W/L = 0{\cdot}87$ from fig. 385, DW. F (✳): *Nucella lapillus*, Hughes (1972), 7, from average of monthly regressions Table 1, assumed $W/L = 0{\cdot}56$ from fig. 1903, DW. G (□): *Nassarius vibex*, our data, 5, W/L measured, AFDW. H (◎): *Polinices duplicatus*, our data, 21, W/L measured, AFDW. I (▽): *Thais haemastoma*, our data, 27, W/L measured, AFDW. J (✸): *L. littorea*, Grahame (1973*a*), 8, from DW-shell height regression, assumed $W/L = 0{\cdot}76$ from fig. 549, DW.



TEXT-FIG. 7. Regression lines for gastropod biomass versus log of operational biovolume. Regression lines are combined from text-figs. 5 and 6.

for many species. In the equations to follow, however, equation 2 can be replaced by any other equation relating size to age should a more accurate one be known.

To determine T from this equation, s_T must be known for each species in question. This requires at least one known age-size relation. In some cases this might be obtained by actually determining the age at death for a few individuals, by counting growth lines, for example. Barring this capability, an alternative approach would be to relate maximum age and maximum size because maximum size data are commonly available for fossil species. This approach is used here. Maximum size in any fossil assemblage, however, is not necessarily equivalent to the maximum size of the species because poor survival may prevent individuals of a species from growing to their maximum size in many areas. Thus, a literature search is essential to verify true maximum size for the species. Maximum age data for modern analogues of many palaeo-species can be found in Comfort (1957), Peterson (1979), and other works, some of which are summarized in Table 1. Within-taxon variability in maximum age may be considerable. Also, sexual dimorphism and environmentally determined differences in growth rate may contribute additional uncertainty (Wilbur and Owen 1964; Fotheringham 1971; Franz 1971). Consequently, for calculations of energy flow of taxa in the Stone City Formation, we use a range of ages at maximum size that available data suggest will bracket the true maximum age. If age-size information is not available, percentage maximum age (using maximum size from the literature as 100% maximum age) might be used (Stanton *et al.* 1981). Use of this method is discussed later.

Energy expended in growth

The amount of energy expended in growth during the animal's lifetime (P_{glt}) can be calculated by converting biomass at death to its energy equivalent in calories. Conversion factors are reviewed by Cummins and Wuycheck (1971) (see Tyler 1973 for additional values). The conversion factors used for subsequent calculations of energy expended in growth are:

Gastropods:	5675 cal·g AFDW⁻¹
Bivalves:	4452 cal·g AFDW⁻¹

Energy expended in respiration

Daily respiration. Energy expended in respiration depends upon the biomass of the individual and of the temperature at which it lives (Prosser 1973). These relations are expressed by the regression lines in text-fig. 8 for species of gastropods and bivalves. Each individual line is for a particular species, observed at a particular temperature. For simplicity, we have divided the data into three temperature ranges, 10±5, 20±5, and 30±5 °C, denoted by the three line weights. Respiration is usually measured in terms of oxygen consumption. The caloric conversion used in the literature ranges from 4·75 to 5·0 cal·ml⁻¹ O_2, depending on the author. The mean of values from Hughes (1971a), Thompson and Bayne (1974), and Bernard (1974), 4·86 cal·ml⁻¹, is used to generate the data in text-fig. 8. The resulting equations relating respiration to biomass are in the form:

$$\log_{10}R = m_R \log_{10}B + b_R \quad (3)$$

where B is biomass in grams and R is respiration in calories per day. Regression equations for the data in text-fig. 8 for each temperature range are:

$$10\pm5\ ^\circ\mathrm{C}\colon \log R = (0{\cdot}8573\pm0{\cdot}0101)\log B + (1{\cdot}4984\pm0{\cdot}0179) \qquad r = 0{\cdot}89 \quad (3a)$$

$$20\pm5\ ^\circ\mathrm{C}\colon \log R = (0{\cdot}9142\pm0{\cdot}0042)\log B + (1{\cdot}7587\pm0{\cdot}0133) \qquad r = 0{\cdot}95 \quad (3b)$$

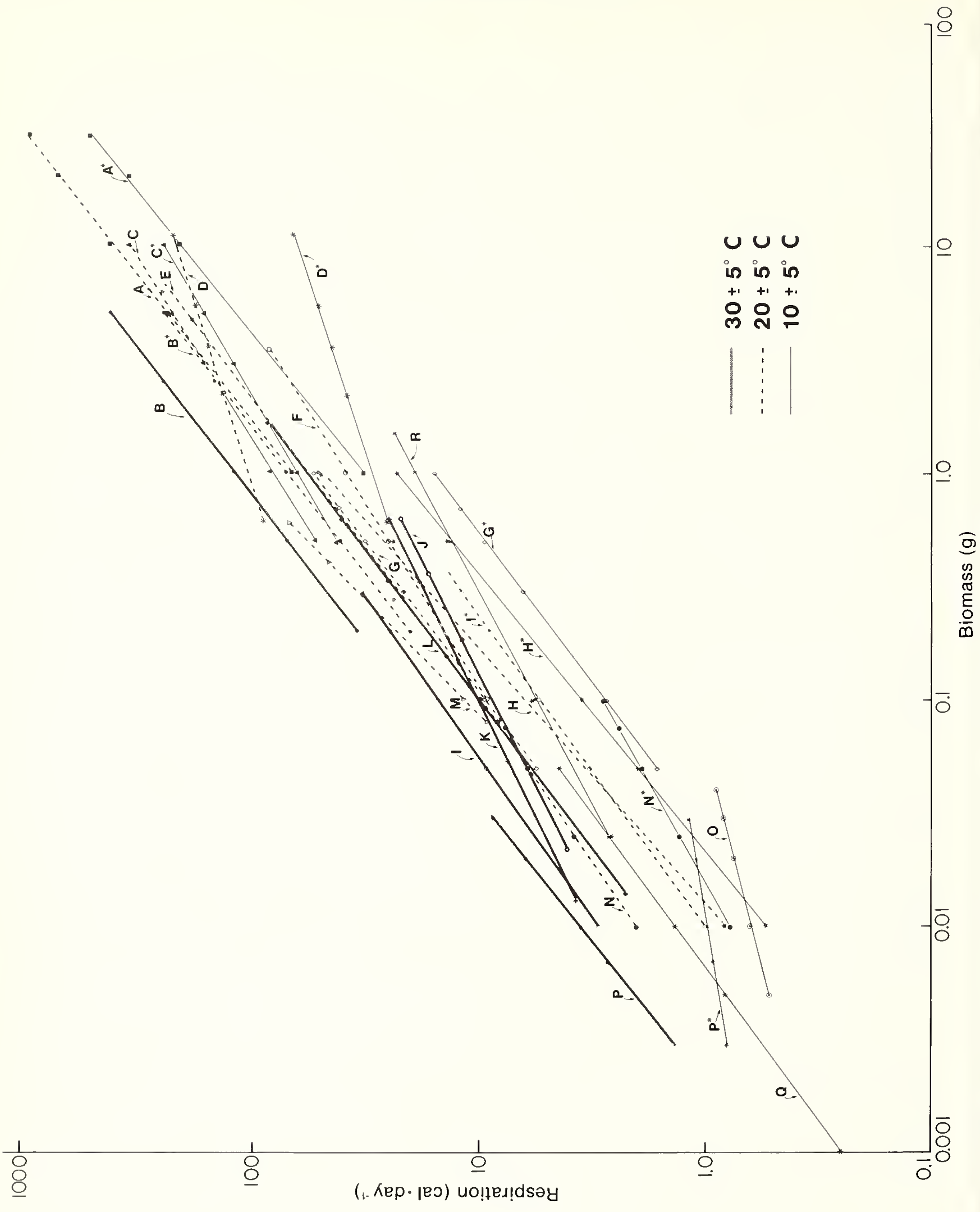
$$30\pm5\ ^\circ\mathrm{C}\colon \log R = (0{\cdot}7736\pm0{\cdot}0073)\log B + (1{\cdot}8943\pm0{\cdot}0169) \qquad r = 0{\cdot}95 \quad (3c)$$

The data for 20 and 30 °C overlap to a considerable extent, whereas the data for 10 °C are clearly below the other two (text-fig. 8). Combining the 20 and 30 °C data sets yields:

$$\log R = (0{\cdot}8375\pm0{\cdot}0029)\log B + (1{\cdot}8152\pm0{\cdot}0087) \qquad r = 0{\cdot}94 \quad (3d)$$

If all three data sets are combined, the regression is:

$$\log R = (1{\cdot}0054\pm0{\cdot}0072)\log B + (1{\cdot}7421\pm0{\cdot}0155) \qquad r = 0{\cdot}82 \quad (3e)$$


Respiration (cal · day⁻¹)
1000
100
10
1.0
0.1
Biomass (g)
0.001
0.01
0.1
1.0
10
100
30 ± 5° C
20 ± 5° C
10 ± 5° C
A*
C
C*
A
E
D
D*
B*
B
F
R
G*
J
G
L
I*
H*
M
H
K
I
N*
O
N
P
P*
Q

Because the data used are selected subsets of considerably larger data sets, confidence limits and correlation coefficients for the regressions are conditional. Differences in the regression lines for individual species might result from the following: (1) The temperature effect, as discussed above. (2) Salinity (Lange *et al.* 1972), food concentration (Thompson and Bayne 1974), oxygen concentration (Staaland 1972), and seasonal cycles. (3) Differences in the amount of activity of the organism during the time respiration was measured (e.g. quiescent vs. active animals—Newell and Pye 1971) and (4) differences in the temperatures of acclimation, acclimatization, and experimentation. The range of values about the 10, 20, and 30 °C regression lines is small, indicating that only temperature is a major source of variability. Furthermore, combining the 20 and 30 °C data does not affect the resulting regression substantially—however, adding the 10 °C data produces a marked change. Thus, it appears reasonable in palaeoecology to use the 10 °C equation for cold-water faunas and the combined 20 and 30 °C equation for temperate-tropical faunas.

These equations can be used to estimate respiration rates for most molluscan species encountered in palaeo-communities. The accuracy of this procedure can be evaluated by comparing calculated values with measured values of respiration (Table 2) for species not included in any of the data sets used for the previous equations. The calculated values of biomass for four such species (Table 2) are within a factor of 1·4 of the measured values. The combined 20 °C + 30 °C respiration equation more accurately predicts respiration at 20 °C than does the 20 °C equation in most cases, whereas the 10 °C + 20 °C + 30 °C equation is clearly inferior. Respiration rates predicted from the 20 °C + 30 °C, or the 10 °C equation are all within a factor of 1·7 of the actual values. Thus, respiration rate can be effectively predicted from shell dimensions using equations 1 and 3.

Lifetime respiration. In palaeoecology, the total energy expended in respiration during the organism's lifetime (R_{lt}) must be determined. This is daily respiration rate (R of equation 3) integrated over the organism's life span, taking into account the change in respiration rate with size as the animal grows.

Age and biovolume are related by the equation.

$$V = S^3 = [s_T \log(T+1)]^3 \tag{4}$$

TEXT-FIG. 8 (*opposite*). Regression lines of respiration rate (in calories per day) versus biomass (in grams) on a log–log scale. Biomass data have been selected to cover the range of biomass used in the referenced data set. The following explanations are ordered as follows: species, source, temperature(s) plotted (lower temperature indicated by *), comments. A (■), A* (■): *Patinopecten yessoensis*, Fuji and Hashizume (1974), 22 °C, 9 °C, data from fig. 2. B (●), B* (●): *Brachidontes demissus plicatulus*, Read (1962), 28·2 °C, 22 °C, from regression equations Table 4. C (▼), C* (▼): *Mytilus edulis*, Read (1962), 19·8 °C, 12 °C, from regression equations Table 2. D (✱), D* (✱): *Mercenaria mercenaria*, Hibbert (1977*b*), 20 °C, 10 °C, from regression equation relating respiration to length and temperature and the length biomass regression of Hibbert (1977*a*). E (☆): *Polinices duplicatus*, Huebner and Edwards, D. C. (1981), 22·7 °C, data from regression of shell-less wet wt.-respiration and diameter-wet wt. Table 1 using AFDW-diameter regression from Edwards and Huebner (1977). F (○): *Mytilus perna*, Bayne (1967), 20 °C, from regression of respiration-DW. G (◇), G* (◇): *Scrobicularia plana*, Hughes (1970), 22·5 °C, 9·5 °C, from regression equation. H (★), H* (★): *Tegula funebralis*, Paine (1971), 17 °C, 10 °C from fig. 1. I (○), I* (○): *Fissurella barbadensis*, Hughes (1971a), 30·2 °C, 21 °C, from regression equations. J (✪): *Nerita versicolor*, Hughes (1971*b*), 30 °C, from respiration-L and L-DW regressions. K (+): *N. tesselata*, Hughes (1971*b*), see J. L (◆): *N. peloronta*, Hughes (1971*b*), see J. M (▽): *Modiolus demissus*, Kuenzler (1961), 20 °C, from fig. 6. N (●), N* (●): *Mya arenaria*, Kennedy and Mihursky (1972), 20 °C, 10 °C, regression for individuals acclimated to experimental temperature Table 2, young only. O (❄): *Macoma balthica*, Kennedy and Mihursky (1972), 10 °C, see N Table 5. P (✳), P* (✳): *Mulinia lateralis*, Kennedy and Mihursky (1972), 30 °C, 10 °C, see N Table 7. Q (✱): *Spisula subtruncata*, Møhlenberg and Kiørboe (1981), 11–14 °C, used regression of respiration to wt. for fed animals. R (X): *Chlamys delicatula*, Mackay and Shumway (1980), 10 °C, used DW–VO regression equation.

TABLE 1. Maximum ages for selected bivalves and gastropods reported since Comfort (1957) exclusive of Peterson (1979).

Species	Suggested maximum age	Source	Species	Suggested Maximum age	Source
Gastropoda			Bivalvia		
Haliotidae					
Haliotis iris	> 10 yr.	Poore (1972)	Nuculanidae		
Patellidae			*Nuculana minuta*	7–8 yr.	Ansell, *et al* (1978)
Acmaea digitalis	8 yr.	Zaika (1970)	*Nuculana pernula*	5 yr.	Ansell, *et al* (1978)
Patella aspera	12 yr.	Thompson, G. B. (1979)	Arcidae		
Trochidae			*Senilia senilis*	9 yr.	Okera (1976)
Margarita helicina	1·67 yr.	Zaika (1970)	Mytilidae		
Tegula funebralis	24–30 yr.	Cockcroft and Forbes (1981)	*Crenomytilus grayanus*	88 yr.	Selin (1980)
Lacunidae			*Mytilus galloprovinciallis*	12 yr.	Zaika (1970)
Lacuna pallidula	< 1 yr.	Zaika (1970)	Ostreidae		
Littorinidae			*Ostrea edulis*	20 yr.	Rodhouse (1978)
Littorina saxatilis	1 yr.	Burke and Mann (1974)	Leptonidae		
Rissoidae			*Mysella planulata*	4 yr.	Franz (1973)
Rissoa parva	0·75 yr.	Wigham (1975)	Cardiidae		
Rissoa splendida	1 yr.	Zaika (1970)	*Cardium edule*	11 yr.	Evans and Tallmark (1977)
Hydrobiidae			*Cerastoderma edule*	14 yr.	Boyden (1972)
Hydrobia neglecta	1·5 yr.	Lassen and Clark (1979)	*Cerastoderma glaucum*	7 yr.	Boyden (1972)
Hydrobia ventrosa	1·5 yr.	Lassen and Clark (1979)	Mactridae		
Hydrobia ulvae	> 2 yr.	Lassen and Clark (1979)	*Spisula elliptica*	1 yr.	Zaika (1970)
Potamididae			*Spisula solidissima*	25 yr.	Jones (1980)
Cerithidea decollata	3–9 yr.	Cockcroft and Forbes (1981)	Tellinidae		
Cerithiidae			*Macoma balthica*	9 yr.	Evans and Tallmark (1977)
Cerithium atratum	1 yr.	Houbrick (1974)	*Macoma balthica*	> 7 yr.	Warwick and Price (1975)
Cerithium eburneum	1 yr.	Houbrick (1974)	*Macoma litoralis*	> 5 yr.	McLachlan (1974)
Cerithium lutosum	1 yr.	Houbrick (1974)	*Tellina martinicensis*	2 yr.	Penzias (1969)
Cerithium muscarum	1 yr.	Houbrick (1974)	*Tellina tenuis*	> 7 yr.	Trevallion (1971)
Diastoma varium	1·5 yr.	Marsh (1976)	Semelidae		
Naticidae			*Abra ovata*	3–4 yr.	Zaika (1970)
Polinices duplicatus	4–7 yr.	Hunter and Grant (1966)	Solecurtidae		
Muricidae			*Tagelus divisus*	2·5 yr.	Fraser (1967)
Ocenebra poulsoni	> 9 yr.	Fotheringham (1971)	Arcticidae		
Shaskyus festivus	> 10 yr.	Fotheringham (1971)	*Arctica islandica*	~ 70 yr.	Jones (1980)
Urosalpinx cinerea	> 4 yr.	Franz (1971)	Veneridae		
Buccinidae			*Anomalocardia squamosa*	2·5 yr.	Morton (1978)
Neptunea antiqua	> 10 yr.	Pearce and Thorson (1967)	*Dosinia hepatica*	6 yr.	McLachlan (1974)
Nassariidae			*Mercenaria mercenaria*	25–40 yr.	Loesch and Haven (1973)
Nassarius reticulatus	> 15 yr.	Tallmark (1980)	*Tapes japonica*	~ 3 yr.	Ohba (1959)
Retusidae			Myidae		
Retusa obtusa	1 yr.	Smith (1967)	*Mya arenaria*	> 17 yr.	Warwick and Price (1975)
			Mya arenaria	12 yr.	Evans and Tallmark (1977)

TABLE 2. Comparison of calculated with measured biomass and respiration values for four bivalves not included in either the biomass or respiration regressions. Predicted values use length as the input datum.

Species	Measured values				Calculated values				Source for measured data, and comments	
	Length (mm)	Biomass (g)	Temperature (°C) at which respiration measured	Respiration (cal/day)	Biomass (g)	Respiration (cal/day)				
						At measured temperature	20° + 30° equation	10° + 20° + 30° equation		
Donax serra	21·8	0·1	20 10	14·93 7·00	0·089	6·28 3·96	8·62	4·85	Dye (1979)	Measured values for respiration and length from author's biomass regression equations
Donax sordidus	24·8	0·1	20 10	15·40 6·42	0·129	8·82 5·44	11·76	7·05	Dye (1979)	Same as for *D. serra*
Aulacomya ater	25·0	0·094	12·5	3·65	0·132	5·55		7·21	Griffiths, C. L. and King (1979*b*)	Measured values from length regressions assuming predicted R is in μl 0_2hr^{-1} (as in Fig. 4) rather than ml·hr^{-1} as stated. Predicted values of R at measured temperature use 10 °C regression equation
Choromytilus meridionalis	25·0	0·110	18 12	10·41 7·39	0·132	9·01 5·55	11·99	7·21	Griffiths, R. J. (1981)	Measured values from (1) regression equation Table 1 for B.L.W.S. at 12 °C + 18 °C; and (2) Avg. of DW–length regressions in Griffiths, R. J. and Buffenstein (1981). Predicted values of R at measured temperature were calculated using 20 °C and 10 °C regression equations

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Lacunidae			*Mytilus galloprovinciallis*	12 yr.	Zaika (1970)
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Cerithium eburneum	1 yr.	Houbrick (1974)	*Macoma litoralis*	> 5 yr.	McLachlan (1974)
Cerithium lutosum	1 yr.	Houbrick (1974)	*Tellina martinicensis*	2 yr.	Penzias (1969)
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Naticidae			*Abra ovata*	3–4 yr.	Zaika (1970)
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Shaskyus festivus	> 10 yr	Fotheringham (1971)	*Arctica islandica*	~ 70 yr	Jones (1980)
Urosalpinx cinerea	> 4 yr	Franz (1971)	Veneridae		
Buccinidae			*Anomalocardia squamosa*	2·5 yr.	Morton (1978)
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Nassariidae			*Mercenaria mercenaria*	25–40 yr.	Loesch and Haven (1973)
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Retusa obtusa	1 yr.	Smith (1967)	*Mya arenaria*	> 17 yr.	Warwick and Price (1975)
			Mya arenaria	12 yr.	Evans and Tallmark (1977)

TABLE 2. Comparison of calculated with measured biomass and respiration values for four bivalves not included in either the biomass or respiration regressions. Predicted values use length as the input datum.

Species	Measured values				Calculated values				Source for measured data, and comments	
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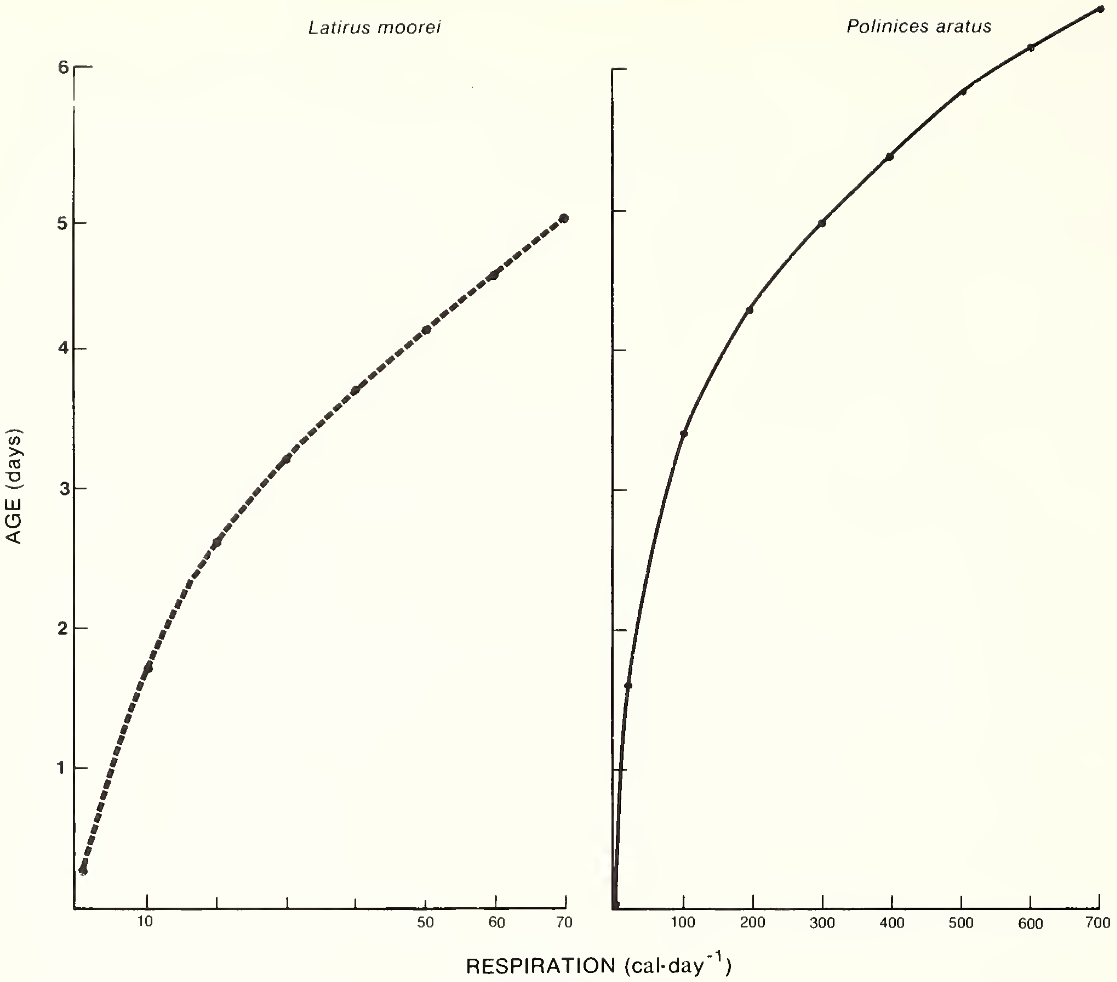
						At measured temperature	20° + 30° equation	10° + 20° + 30° equation		
Donax serra	21·8	0·1	20 10	14·93 7 00	0·089	6·28 3 96	8·62	4 85	Dye (1979)	Measured values for respiration and length from author's biomass regression equations
Donax sordidus	24 8	0·1	20 10	15 40 6·42	0·129	8·82 5·44	11 76	7·05	Dye (1979)	Same as for *D. serra*
Aulacomya ater	25·0	0·094	12·5	3·65	0·132	5·55		7·21	Griffiths, C. L. and King (1979*b*)	Measured values from length regressions assuming predicted *R* is in $\mu l\ O_2 hr^{-1}$ (as in Fig. 4) rather than $ml \cdot hr^{-1}$ as stated. Predicted values of *R* at measured temperature use 10 °C regression equation
Choromytilus meridionalis	25·0	0 110	18 12	10·41 7·39	0 132	9 01 5·55	11·99	7 21	Griffiths, R. J. (1981)	Measured values from (1) regression equation Table 1 for B.L.W.S. at 12 °C + 18 °C; and (2) Avg. of DW-length regressions in Griffiths, R. J. and Buffenstein (1981). Predicted values of *R* at measured temperature were calculated using 20 °C and 10 °C regression equations



TEXT-FIG. 9. The change in respiration rate (in cal · day^{-1} estimated using equation 6), with age (in days estimated using equation 2 and Table 5), for two species from Stone City.

Combining equation 4 with equations 1 and 3 yields:

$$\log R = m_R(m_B \log\{[s_T \log(T+1)]^3\} + b_B) + b_R \qquad (5)$$

Taking the antilog and rearranging the constants yields:

$$R = ((s_T)^{3m_R m_B})(10^{m_R b_B + b_R})([\log(T+1)]^{3m_R m_B}) \qquad (6)$$

Equation 6 relates respiration to age at any specified age [in days because R is measured in cal · day^{-1} (equation 3)]. The relationship of respiration to age as predicted by this equation is shown in text-fig. 9. Respiration increases with age as the individual grows, but at a decreasing rate because growth rate decreases with age.

To calculate the total respiration during an organism's life span, equation 6 is integrated from birth, t_0, to death, t_n:

$$R_{lt} = \int_{t_0}^{t_n} \{(s_T{}^{3m_R m_B})(10^{m_R b_B + b_R})([\log(T+1)]^{3m_R m_B})\}\, dT \qquad (7)$$

Equation 7 cannot be solved directly unless $3m_R m_B$ is an integer. When using equations 1a, b and 3a–e, it is not. Therefore we calculated R_{lt} by summing consecutive values of R from t_0 to t_n, using a computer and one-, ten-, or thirty-day time-steps depending on the age of the individual. The estimation of R_{lt} depends on the accuracy with which age can be estimated from size and will be less accurate for older than for younger individuals because age increments are represented by smaller and smaller size increments as growth rate declines with age.

Energy expended in reproduction (P_{r})

Energy expended in reproduction can be estimated if the size at maturity and a relationship between P_{r} and either P_{g} or R are known. Data on energy used for reproduction are less numerous and probably less accurate than data on energy used for growth or for respiration. Available data for bivalves and gastropods, and their size at maturity as a percentage of maximum size, are presented in Table 3. Maturity is defined as age at initial gonadal development, rather than age at first spawning. Most values for size at maturity are between 40 and 70% of maximum size and average 44 and 51% for bivalves and gastropods respectively. This difference is not significant ($\alpha = 0{\cdot}5$, Student's t-test).

Energy expended in reproduction, as a value equivalent to a percentage of the energy expended in respiration, ranges from 3 to 40% for bivalves, but most values are between 10 and 30%, averaging 18%. Values range from 2 to 26% for gastropods, with most values below 10%, averaging 6·8%. The difference between bivalves and gastropods is significant ($0{\cdot}05 < P < 0{\cdot}10$; Student's t-test). The data, however, are insufficient to determine whether this difference is real or merely a result of a small data base. In the following calculations the average values for the two classes are used.

The energy expended by an animal in reproduction in its lifetime (P_{rlt}) is equivalent to a percentage of the energy expended in respiration during that part of its life subsequent to attaining sexual maturity. Thus,

$$P_{\mathrm{r}} = 18 \text{ or } 6{\cdot}8\,\% \text{ of } \left[\int_{t_0}^{t_n} R\,\mathrm{d}R - \int_{t_0}^{t_m} R\,\mathrm{d}R\right] \qquad (8)$$

where t_0 is age at birth; t_n age at death; t_m age at maturity. The first integral corresponds to R_{lt} from equation 7.

Caveats associated with the data in Table 3 include the following: (1) differences in food supply affect fecundity (Spight and Emlen 1976). (2) Taxa which produce more than two clutches per year are not included. Equation 8 may not apply to such species (Borkowski 1971). (3) We assume that both males and females utilize energy at the same rate, although this is not always the case (Grahame 1973*a*). (4) Iteroparous species may differ from semelparous species (Browne and Russell-Hunter 1978); most species in Table 3 reproduce in more than one year. (5) The transition from immaturity to maturity in long-lived species may be gradual over a period of years, during which time reproductive output gradually increases to adult levels. This transition period is not included in equation 8, which treats reproduction as an all or nothing phenomenon beginning at 44 or 51% maximum size. (6) Many values in Table 3 are means of populations including non-reproducing juveniles as well as reproducing adults. This is not likely to be a significant factor in most cases because adult respiration is significantly greater per individual than juvenile respiration, and the data are presented as a percentage of respiration—however, the data of Paine (1971) and Hibbert (1977*b*) illustrate the potential error introduced from this source.

Estimation of energy assimilated (A)

The total assimilated energy during an individual's lifetime (A_{lt}) is:

$$A_{\mathrm{lt}} = P_{\mathrm{glt}} + R_{\mathrm{lt}} + P_{\mathrm{rlt}} \qquad (9)$$

Estimation of ingestion (I)

Ingestion during an organism's lifetime (I_{lt}) can be estimated using an assimilation efficiency (A/I):

$$I_{\mathrm{lt}} = A_{\mathrm{lt}} \cdot (A/I)^{-1} \qquad (10)$$

TABLE 3. The amount of energy expended per year in reproduction as a percentage of that expended in respiration (i.e. 40% indicates that the energy expended in reproduction was equivalent to 40% of that expended for respiration during the year studied) and the size at maturity as a percentage of maximum size in molluscs.

Species	Size at maturity	Energy expended in reproduction	Comments	Source
Bivalvia				
Aulacomya ater	18%	—	—	Griffiths, C. L. and King (1979*a*)
Choromytilus meridionalis	54%	0, 40, 37, 36, 35%. Avg. yrs. 2–5 = 37%	From Table 2. Energy expended is for age classes 1, 2, 3, 4, 5 yr. respectively	Griffiths, R. J. (1981)
Crassostrea virginica	40%	12%	Average of monthly surveys, Table 2, for a population with $>$ 50% juveniles	Dame (1976)
Mercenaria mercenaria	43%	0, 0, 25, 32, 28, 28, 26, 29%. Avg. of 8 = 21%; of last 6 = 28%	Energy expended is for age classes (from left to right, top to bottom) 1, 2, 3, 4, 5, 6, 7, 8 yr.	Hibbert (1977*b*)
Modiolus demissus	—	7·8%	Population mean with most biomass as adults although $\sim$ 25% of the individuals were juveniles	Kuenzler (1961)
Mytilus californianus	42%	7, 7, 6%	Energy expended for age classes 1, 2, 3 yr, respectively	Fox and Coe (1943)
Ostrea edulis	—	24, 27, 35, 35%. Avg. = 30%	Energy expended for age classes 5, 10, 15, 20 yr respectively	Rodhouse (1978)
Patinopecten yessoensis	—	3, 10, 15%. Avg. of 3 = 9%; of last 2 = 13%	Energy expended for age classes 1, 2, 3 yr, respectively	Fuji and Hashizume (1974)
Scrobicularia plana	—	13·4, 7·6%. Avg. = 11%	Population means of two separate populations	Hughes (1970)
Tagelus divisus	37%	—	—	Fraser (1967)
Tellina martinicensis	77%	—	—	Penzias (1969)
Tellina tenuis	—	9·7, 21·8%. Avg. = 15·8%	Population means of one population in consecutive years.	Trevallion (1971)
Bivalve average	44%	18·0%	Using all averaged data excluding yrs. 1 and 2 of Hibbert (1977*b*) and yr. 1 of Fuji and Hashizume (1974)	
Gastropoda				
Fissurella barbadensis	33%	3·8%	Population mean with most individuals adults	Hughes (1971*b*)
Littorina littorea	40%	—	—	Grahame (1973*a*)
Nassarius reticulatus	50%	—	—	Tallmark (1980)
Neptunea antiqua	73%	—	—	Pearce and Thorson (1967)
Nerita peloronta	45%	2·2, 2·9%. Avg. = 2·6%	Population means of two separate populations, left population has more juveniles than right population	Hughes (1971*b*)
Nerita tesselata	56%	3·9%	Population mean of population with $\sim$ 50% adult individuals	Hughes (1971*b*)
Nerita versicolor	64%	1·8%	Population mean of population with $\sim$ 50% adult individuals	Hughes (1971*b*)
Nucella lapillus	57%	33, 18.3%. Avg. = 26%	Population means of two separate populations in which most individuals were adults	Hughes (1972)
Petella aspera	34%	—	—	Thompson (1979)
Tegula funebralis	54%	0·2, 2·9%	Population means of two separate populations: left with 93% of individuals juveniles; right with 17% juveniles	Paine (1971)
Thais emarginata	63%	—	—	Spight and Emlen (1976)
Thais lamellosa	40%	—	—	Spight and Emlen (1976)
Gastropod average	51%	6·8%	Using all averaged data but excluding 0·2% of Paine (1971)	

Assimilation efficiencies that have been measured for living molluscs are presented in Table 4; they are nearly equal for bivalves and gastropods, averaging 0·53 and 0·54 respectively. The data do not support Welch's (1968) suggestion that carnivores have a higher assimilation efficiency than herbivores-detritivores although information on carnivorous molluscs is scarce. Caveats concerning the data in Table 4 include the following. (1) Assimilation efficiency varies with food concentration and food quality (Thompson and Bayne 1974; Kofoed 1975). (2) Some values have been determined

TABLE 4. Assimilation efficiencies for bivalves and gastropods.

Species	Assimilation efficiency	Comments	Source
Bivalvia			
Choromytilus meridionalis	0·18, 0·15, 0·16, 0·16, 0.16. Avg. = 0·16	From Table 2, for age classes 1, 2, 3, 4, 5 yr, respectively	Griffiths, R. J. (1981)
Mercenaria mercenaria	0·39	Population mean	Hibbert (1977*b*)
Mytilus californianus	0·8, 0·77, 0·78. Avg. = 0·78	For age classes 1, 2, 3 yr, respectively	Fox and Coe (1943)
Mytilus californianus	0·59	Table 5	Elvin and Gonor (1979)
Mytilus edulis	0·39	Value at peak number of calories assimilated—values varied from 0·20 to 0·90	Thompson, R. J. and Bayne (1974)
Patinopecten yessoensis	0·79, 0·65, 0·68. Avg. = 0·71	For age classes 1, 2, 3 yr, respectively	Fuji and Hashizume (1974)
Scrobicularia plana	0·61, 0·60. Avg. = 0·61	Population means	Hughes (1970)
Spisula subtruncata	0·60	Average of Table 4	Mohlenberg and Kiorboe (1981)
All bivalves	0·60		Edwards, R. R. C. (1973)
Average bivalves	0.53		
Gastropoda			
Fissurella barbadensis	0·34	Population mean	Hughes (1971*a*)
Hydrobia ventrosa	0·53	Average value from Table 1	Kofoed (1975)
Littorina irrorata	0·45		Odum and Smalley (1959)
Littorina littorea	0·86	Mean of values for cal. (%), Table 2	Grahame (1973*b*)
Nerita tesselata	0·40	Population mean	Hughes (1971*b*)
Nerita peloronta	0·41, 0·43. Avg. = 0·42	Population means	Hughes (1971*b*)
Nerita versicolor	0·39	Population mean	Hughes (1971*b*)
Polinices duplicatus	0·70, 0·61, 0·74. Avg. = 0·68	For age classes 1–2, 2–3, 3–4 yr, respectively	Huebner and Edwards, D. C. (1981)
Tegula funebralis	0·71, 0·70. Avg. = 0·70	Population means	Paine (1971)
All gastropods	0·60		Edwards, R. R. C. (1973)
Average gastropods	0·54		
Average total	0·54		
Other			
All carnivores	0·58		Welch (1968)
All herbivores-detritivores	0·43		Welch (1968)

from measurements in mg(%), others in cal(%). (3) Few values include reproduction; of those that do, some are population means that include juveniles as well as adults. (4) Few data are available for carnivores, deposit feeders, or species with short ($<$ 1 yr) life spans. Nevertheless, the available data indicate that ingestion can be predicted within 30% of the measured values using $A/I = 0{\cdot}54$ for the two classes of molluscs.

Accuracy of estimation

Essentially no data exist in the ecologic literature for the parameters P_{rlt}, R_{lt}, A_{lt}, and I_{lt}; thus a check of the accuracy of these estimations is difficult beyond that considered in Table 2. Alimov (1983), however, from an admittedly sparse data base, suggested that the energy utilized during postlarval development by invertebrates should be about 2·5 times the adult biomass (expressed in energy units). Our calculations of energy flow can be compared to Alimov's (1983) prediction by taking biomass at sexual maturity calculated from equation 1 and Table 3 as adult biomass and using the

TABLE 5. Age, biomass, and energy-flow parameters for populations of four gastropods and one bivalve from the Stone City Formation. P_{glt} is energy expended in growth, lifetime; R_{lt}, energy expended in respiration, lifetime; P_{rlt}, energy expended in reproduction, lifetime; A_{lt}, assimilated energy, lifetime; I_{lt}, ingested energy, lifetime. Value for total number of individuals collected is from Stanton and Nelson (1980). Total biomass is the sum of individual biomasses as determined by equations 1a and 1b. Biovolumes for calculating biomass are computed using $V = \frac{1}{3}\cdot\pi\cdot(W/2)^2\cdot L$ for *Polinices aratus*, *Latirus moorei*, and *Hesperiturris nodocarinatus*, $V = \pi(W/2)^2L$ for *Retusa kellogii*, and $V = L^3$ for *Notocorbula texana*. The L and W used are the mean length and width for each size class because the size class intervals were small (Bergh 1974). Maximum sizes are from a compilation of data in Stanton *et al.* (1981), Gardner (1945), Harris (1937), and Palmer, K. V. W. (1937). Estimates for maximum age (T) attained by each species are from Table 1 and Peterson (1979). For the turrid and fasciolariid they are based on the assumption that most neogastropods have ten to fifteen years maximum ages; for the corbulid, that most bivalves of this size and opportunistic life-style (Zarkanellas 1979, Rainer 1982) live less than five years; for the naticid, that its maximum size is less then most *Polinices*, and, therefore, that its maximum age may also he below values in Table 1. The individuals surviving to reproductive age are those that reach 44% of maximum size (bivalves) and 51% of maximum size (gastropods). R_{lt}, P_{rlt}, A_{lt}, and I_{lt}, because they are summed over the lifetime of the organism, depend strongly upon the age of each individual. Maximum age in each case, however, is not well known, therefore calculations are made using the probable range limits (T) of maximum age for each species. Energy expended in respiration (R_{lt}) is based on the 20 °C + 30 °C regression. Calculation of P_{rlt} uses the percentages of 6·8% for gastropods and 18% for bivalves from equation 8. Ingestion (in calories) (I_{lt}) is determined from A_{lt} using an assimilation efficiency (A/I) of 0·54. Ingestion is converted from calories to grams using the gram/calorie conversions from Cummins and Wuycheck (1971) taking into account the probable diet of each species: *P. aratus*—molluscan prey (Stanton and Nelson 1980) at 5492 cal·g AFDW^{-1}; *L. moorei*—mostly molluscan and annelidan prey (Paine 1963) at 5033 cal·g AFDW^{-1}; *H. nodocarinatus*—annelidan prey (Maes 1983) at 4700 cal·g AFDW^{-1}; *R. kellogii*—microconsumer prey (Smith 1967) at 4958 cal·AFDW^{-1}; *N. texana*—algal prey at 4469 cal·g AFDW^{-1}.

Species	Total number of individuals collected	Biomass (g)	P_{glt} (cal)	Maximum size (mm)	Maximum age (yr)	Number surviving to reproductive age		R_{lt} (cal)	P_{rlt} (cal)	A_{lt} (cal)	I_{lt} (cal)	I_{lt} (g)
Polinices aratus	881	3·12	17 696	8·5 (Stanton *et al.* 1981)	2·5–5·0	22	$T = 2·5$	13 389	735	31 820	58 926	10·73
							$T = 5·0$	24 598	1422	43 716	80 956	14·74
Latirus moorei	152	1·41	7985	38·0 (Gardner 1945)	10·0–15·0	0	$T = 10·0$	2336	0	10 321	19 113	3·80
							$T = 15·0$	2809	0	10 794	19 989	3·97
Heperiturris nodocarinatus	137	0·53	3009	17·0 (Stanton *et al.* 1981)	10·0–15·0	19	$T = 10·0$	45 299	2993	51 301	95 002	20·20
							$T = 15·0$	67 873	4437	75 319	139 480	29·68
Retusa kellogii	191	0·72	4067	7·5 (Stanton *et al.* 1981)	1·0–2·0	126	$T = 1·0$	6050	320	10 437	19 328	3·90
							$T = 2·0$	10 947	605	15 619	28 924	5·83
Notocorbula texana	1140	1·29	5733	11·5 (Gardner 1945)	1·0–5·0	321	$T = 1·0$	4462	643	10 838	20 070	4·49
							$T = 5·0$	15 862	2538	24 133	44 691	10·00

TABLE 5. Age, biomass, and energy-flow parameters for populations of four gastropods and one bivalve from the Stone City Formation. P_{glt} is energy expended in growth, lifetime; R_{lt}, energy expended in respiration, lifetime; P_{rlt}, energy expended in reproduction, lifetime; A_{lt}, assimilated energy, lifetime; I_{lt}, ingested energy, lifetime. Value for total number of individuals collected is from Stanton and Nelson (1980). Total biomass is the sum of individual biomasses as determined by equations 1a and 1b. Biovolumes for calculating biomass are computed using $V = \frac{1}{3} \cdot \pi \cdot (W/2)^2 \cdot L$ for *Polinices aratus*, *Latirus moorei*, and *Hesperiturris nodocarinatus*, $V = \pi(W/2)^2 L$ for *Retusa kellogii*, and $V = L^3$ for *Notocorbula texana*. The L and W used are the mean length and width for each size class because the size class intervals were small (Bergh 1974). Maximum sizes are from a compilation of data in Stanton *et al.* (1981), Gardner (1945), Harris (1937), and Palmer, K. V. W. (1937). Estimates for maximum age (T) attained by each species are from Table 1 and Peterson (1979). For the turrid and fasciolariid they are based on the assumption that most neogastropods have ten to fifteen years maximum ages; for the corbulid, that most bivalves of this size and opportunistic life-style (Zarkanellas 1979; Rainer 1982) live less than five years; for the naticid, that its maximum size is less then most *Polinices*, and, therefore, that its maximum age may also be below values in Table 1. The individuals surviving to reproductive age are those that reach 44% of maximum size (bivalves) and 51% of maximum size (gastropods). R_{lt}, P_{rlt}, A_{lt}, and I_{lt}, because they are summed over the lifetime of the organism, depend strongly upon the age of each individual. Maximum age in each case, however, is not well known; therefore calculations are made using the probable range limits (T) of maximum age for each species. Energy expended in respiration (R_{lt}) is based on the 20 °C + 30 °C regression. Calculation of P_{rlt} uses the percentages of 6·8% for gastropods and 18% for bivalves from equation 8. Ingestion (in calories) (I_{lt}) is determined from A_{lt} using an assimilation efficiency (A/I) of 0·54. Ingestion is converted from calories to grams using the gram/calorie conversions from Cummins and Wuycheck (1971) taking into account the probable diet of each species: *P. aratus*—molluscan prey (Stanton and Nelson 1980) at 5492 cal · g AFDW^{-1}; *L. moorei*—mostly molluscan and annelidan prey (Paine 1963) at 5033 cal · g AFDW^{-1}; *H. nodocarinatus*—annelidan prey (Maes 1983) at 4700 cal · g AFDW^{-1}; *R. kellogii*—microconsumer prey (Smith 1967) at 4958 cal · AFDW^{-1}; *N. texana*—algal prey at 4469 cal · g AFDW^{-1}.

Species	Total number of individuals collected	Biomass (g)	P_{glt} (cal)	Maximum size (mm)	Maximum age (yr.)	Number surviving to reproductive age		R_{lt} (cal)	P_{rlt} (cal)	A_{lt} (cal)	I_{lt} (cal)	I_{lt} (g)
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							$T = 5{\cdot}0$	15 862	2538	24 133	44 691	10·00

value of I_{lt} from birth until sexual maturity as the energy utilized during postlarval development. We have used data for the five species from Stone City discussed subsequently (Table 5) to compute the energy utilized during postlarval development from our equations. The values predicted from these equations are consistently within a factor of 1·8 or less of those predicted using Alimov's (1983) method. The fact that Alimov's (1983) method of calculation and data set are completely different from those used here, but yield similar conclusions, suggests that the accuracy of our estimates is substantially better than the sum of the potential errors of each step would suggest. Although none of the individual calculations is error free, the least accurate estimations are, almost certainly, s_T, the species-specific constant relating size to age, and P_{rlt}, the energy expended in reproduction. Increased accuracy in the latter requires a substantially increased data base, whereas increased accuracy in the determination of s_T requires the use of methods for determining age at any size for fossil molluscs that are substantially better than the maximum age-maximum size relation used here.

APPLICATION OF ENERGY FLOW—THE STONE CITY FORMATION (EOCENE)

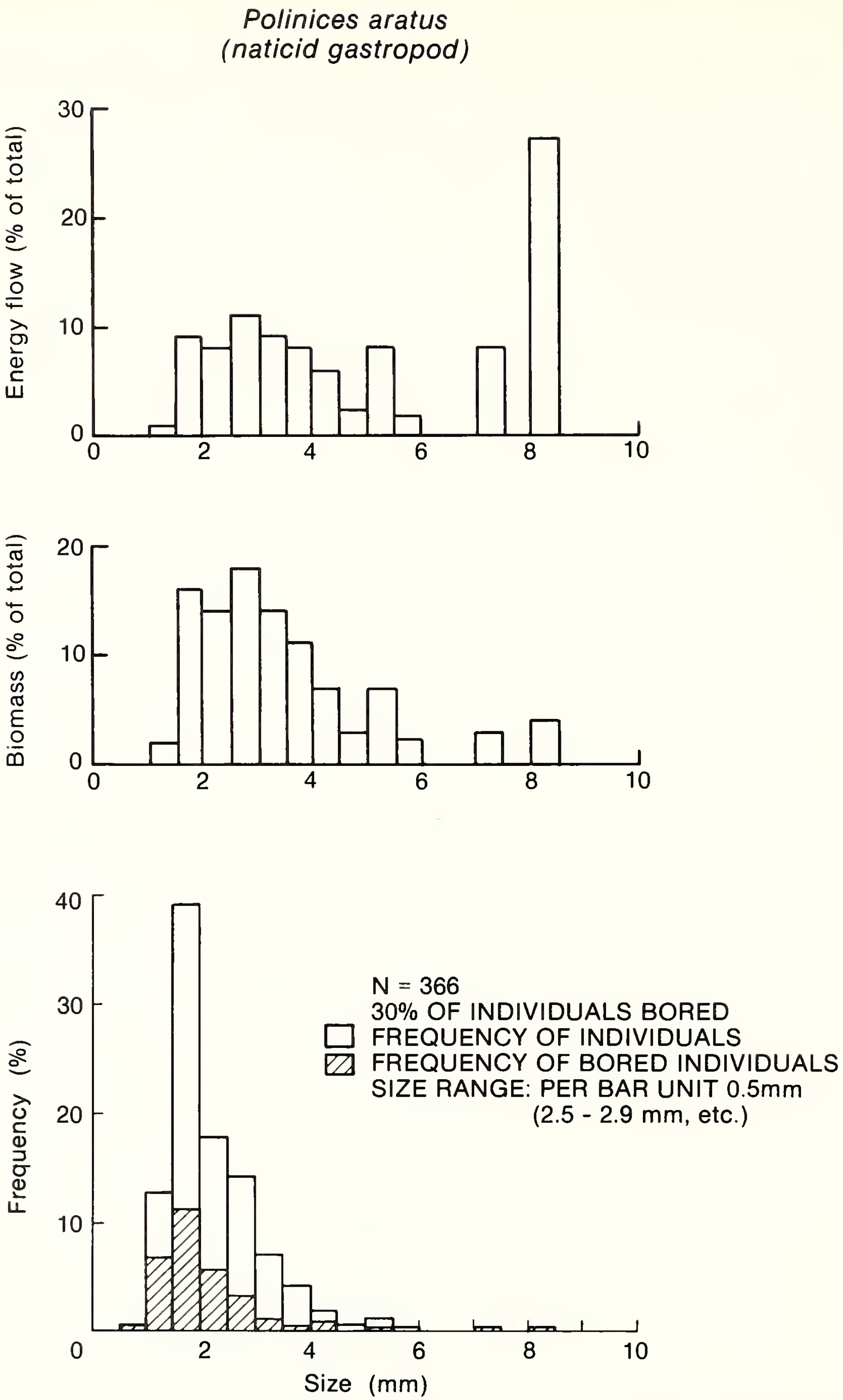
Introduction

Four carnivorous gastropods and one bivalve from the Stone City Formation were analysed to demonstrate the application of energy flow in describing and interpreting palaeo-communities. The species are (1) *P. aratus*, a naticid gastropod characterized by high abundance, a relatively short life span and a high juvenile mortality rate in this assemblage (text-fig. 10); (2) *Latirus moorei*, a fasciolariid, and *H. nodocarinatus*, a turrid; common large gastropods that attained maximum sizes and, probably, maximum ages considerably greater than that of *P. aratus*, and which have relatively high percentages of larger individuals in the size-frequency distributions (text-figs. 11, 12); (3) *Retusa kellogii*, a small, short-lived, retusid gastropod with a high percentage of relatively large individuals in its size-frequency distribution (text-fig. 13); and (4) *Notocorbula texana*, an abundant corbulid bivalve that was an important food source for *P. aratus* (text-fig. 14). Stanton and Nelson (1980) discussed the location of the outcrop, method of collection and initial data analysis. Previous trophic reconstructions of the Stone City community were based on the numerical abundance of the species present (Stanton and Nelson 1980) and their biovolume (Stanton *et al.* 1981).

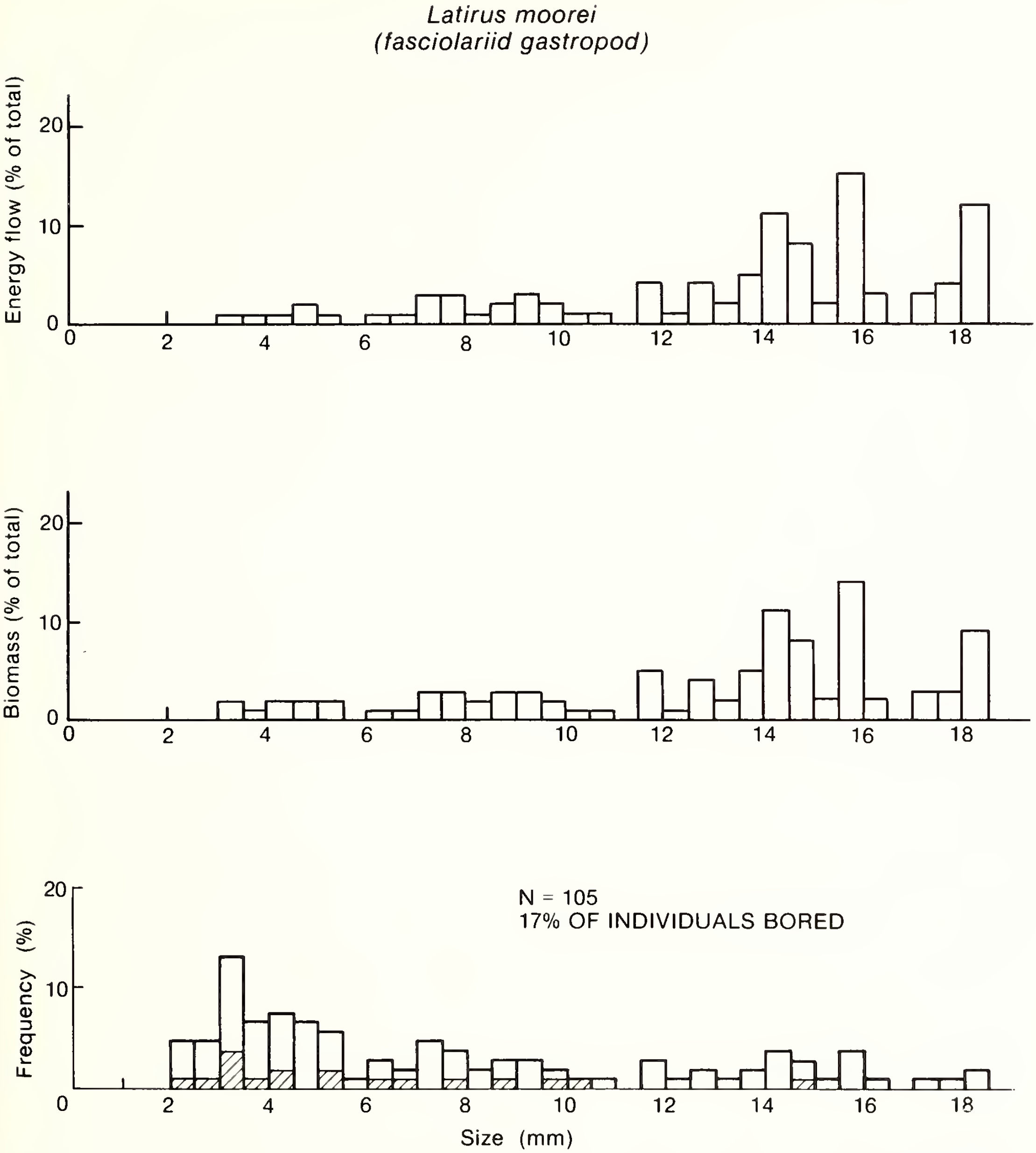
Calculations of energy flow

Age, biomass, and energy flow parameters for these five species (Table 5) have been calculated by the procedures described in the first part of this paper. Two sets of calculations are made for each species to bracket the range of probable maximum ages. The size-frequency distributions and the percentages of total biomass and energy flow in each size class for each species are presented in text-figs. 10–14. The relative importance of the species differs greatly, depending on whether numerical abundance, biomass, or energy flow data are used. Ranking of the species by numerical abundance yields: (1) *N. texana*, (2) *P. aratus*, (3) *R. kellogii*, (4) *L. moorei*, and (5) *H. nodocarinatus*. The ranking by biomass is (1) *P. aratus*, (2) *L. moorei*, (3) *N. texana*, (4) *R. kellogii*, (5) *H. nodocarinatus*. Both *P. aratus* and *L. moorei* are less abundant than *N. texana* but have a greater total biomass because biomass per individual is considerably greater. Ranking of the species by the biomass of prey ingested yields: (1) *H. nodocarinatus*, (2) *P. aratus*, (3) *N. texana*, (4) *R. kellogii*, (5) *L. moorei*. *H. nodocarinatus* had the fewest individuals and smallest biomass, but a number of the individuals lived to near maximum age, reproducing, respiring, and consuming prey for ten plus years. These few individuals consumed as much prey as the more numerous, but shorter-lived individuals of *P. aratus*. Individuals of *L. moorei* grew as large as those of *H. nodocarinatus*, but none reached reproductive age. Consequently, energy expended on growth (P_{glt}) was similar for the two species, but respiratory and reproductive energy expenditures by *L. moorei* were well below that of *H. nodocarinatus*. *R. kellogii*, though small and short lived, had a 66% survival to reproductive age. Consequently, because of the greater energy expended in respiration and reproduction, its estimated prey consumption is comparable to that of *L. moorei* in spite of its smaller size. *P. aratus* was abundant, but consisted

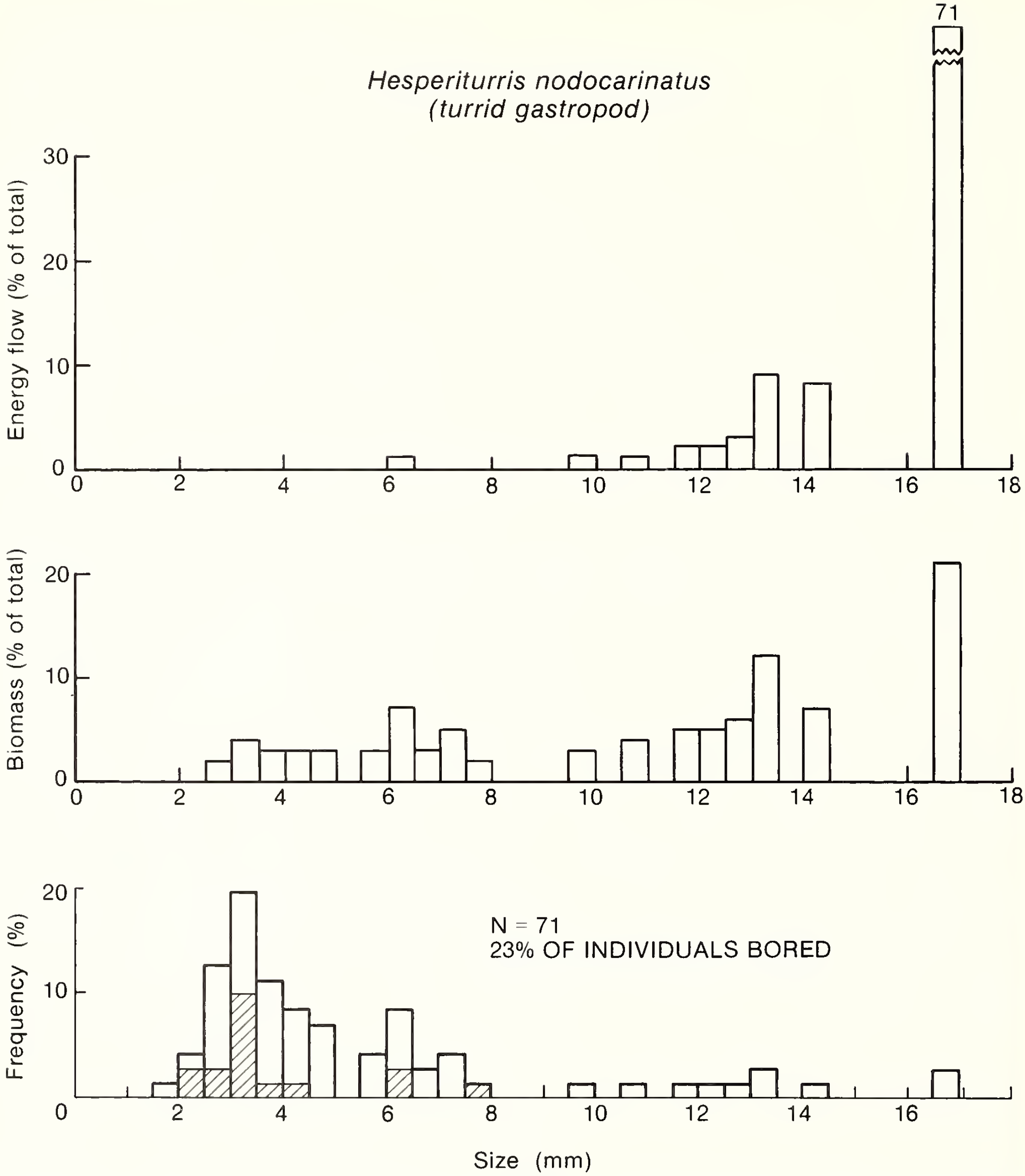
[*Text continues on page 27.*]



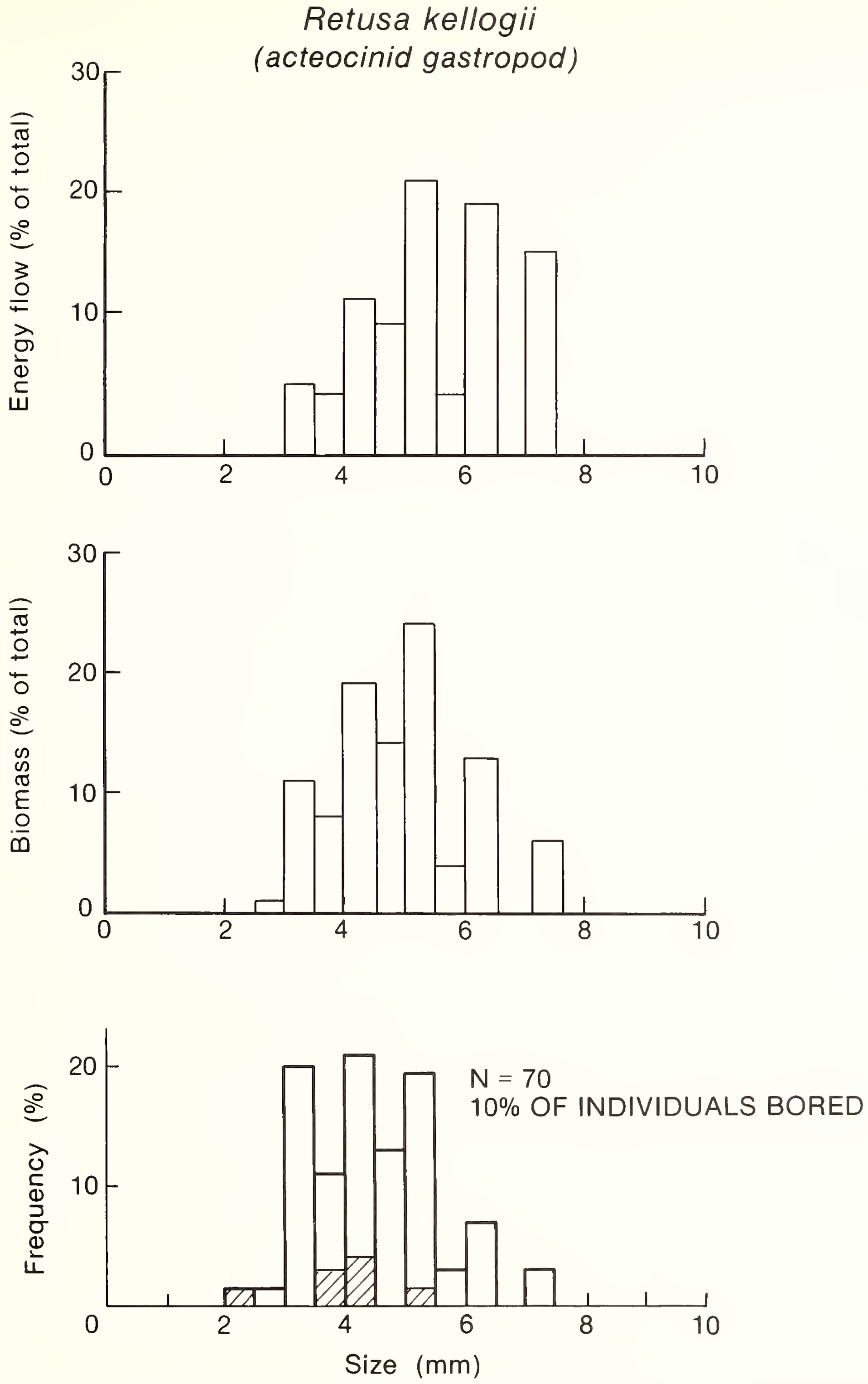
TEXT-FIG. 10. Lower, size-frequency distribution from Stanton *et al.* (1981); middle, percentage of total biomass in each size class; and upper, percentage of total population energy flow (= percentage of total prey ingested) in each size class for the naticid gastropod, *Polinices aratus.*



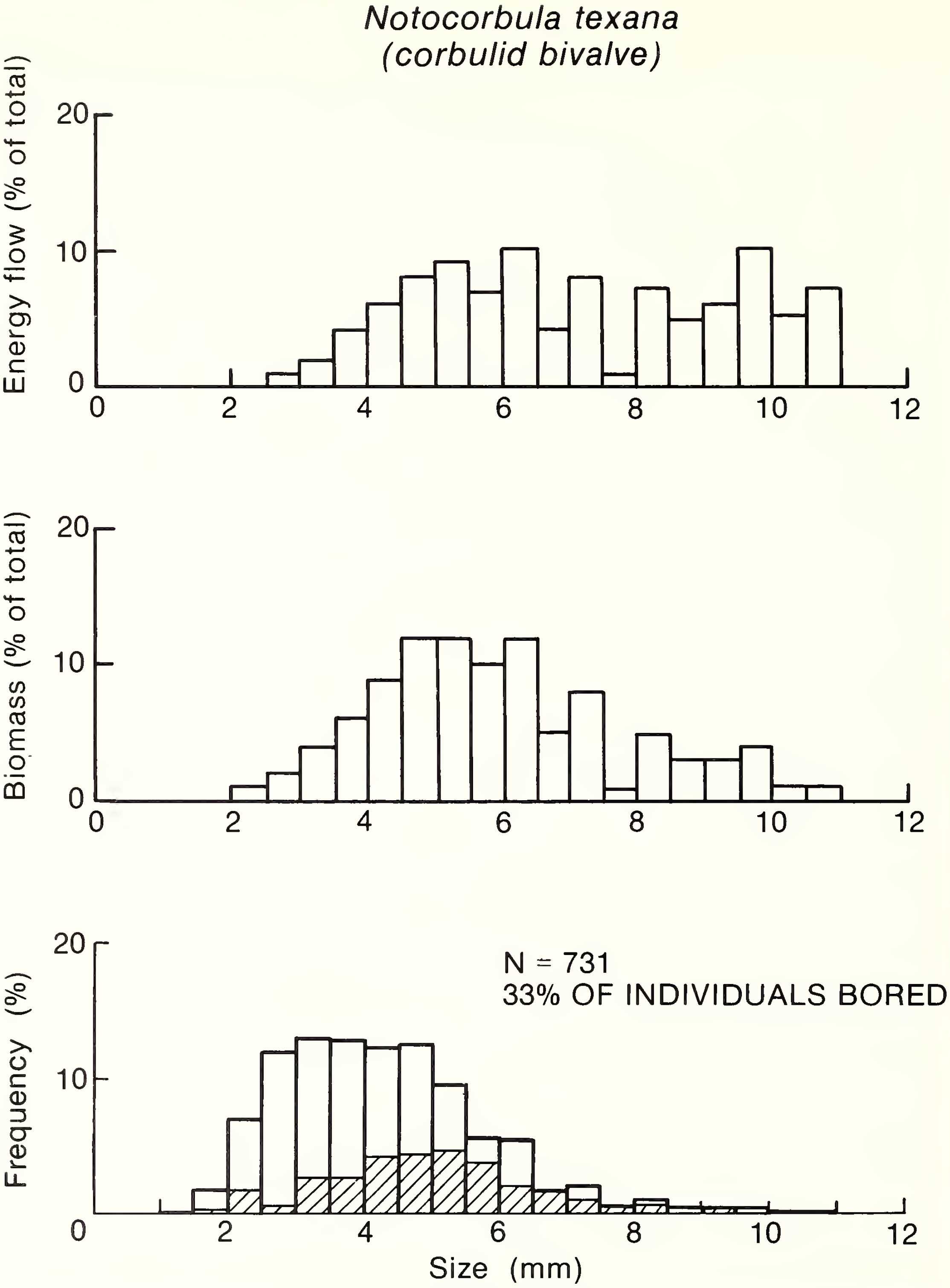
TEXT-FIG. 11. Lower, size-frequency distribution from Stanton *et al.* (1981); middle, percentage of total biomass in each size class; and upper, percentage of total population energy flow (= percentage of total prey ingested) in each size class for the fasciolariid gastropod, *Latirus moorei*.



TEXT-FIG. 12. Lower, size-frequency distribution from Stanton *et al.* (1981); middle, percentage of total biomass in each size class; and upper, percentage of total population energy flow (= percentage of total prey ingested) in each size class for the turrid gastropod, *Hesperiturris nodocarinatus*.



TEXT-FIG. 13. Lower, size-frequency distribution from Stanton *et al.* (1981); middle, percentage of total biomass in each size class; and upper, percentage of total population energy flow (= percentage of total prey ingested) in each size class for the retusid gastropod, *Retusa kellogii.*



TEXT-FIG. 14. Lower, size-frequency distribution from Stanton *et al.* (1981); middle, percentage of total biomass in each size class; and upper, percentage of total population energy flow (= percentage of total prey ingested) in each size class for the corbulid bivalve, *Notocorbula texana*.

largely of small, non-reproducing individuals; yet a few individuals also lived to approximately maximum age. The large amount of energy expended in growth by the many juveniles plus the large amount of energy expended in respiration by the long-lived individuals results in a large predicted prey consumption, second only to that of *H. nodocarinatus*.

This brief analysis of these five species from Stone City indicates how species-specific differences in abundance, size-frequency distribution, survivorship, and maximum age can produce rankings based on energy flow that are very different from those based on numerical abundance or biomass. Trophic reconstructions based on abundance (Hoffman *et al.* 1978; Stanton and Nelson 1980) or on the trophic nucleus as determined from abundance (Antia 1977; Stanton *et al.* 1981) provide a limited view of the community. The relative importance of the various size classes shifts markedly if biomass or energy flow is used rather than abundance (text-figs. 10–14). Use of biomass emphasizes the larger individuals at the expense of the usually more abundant smaller individuals. Conversion to energy flow emphasizes the larger individuals even more. In species such as *H. nodocarinatus*, where some individuals reached near-maximum age, the bulk of the energy flow is accounted for by the largest few size classes.

Thus, the largest, oldest individuals, although numerically of minor importance, are of overwhelming importance in the community's trophic structure. This not only illustrates the danger of depending on numerical abundance data in palaeoecology, but also emphasizes the significance of the larger individuals, which may be most likely to survive taphonomic destruction. For the five species in Table 5, for example, if taphonomic processes had reduced by one-half the number of individuals that were smaller than 50% of the largest size found in the assemblage, the values of energy flow would have been reduced by less than 20%.

Palaeoecologic efficiencies

Stanton *et al.* (1981) discussed the possibility that trophic reconstructions can be used to examine the importance of that portion of the community that is not preserved. In most communities, most of the individuals will not be preserved because they do not have mineralized skeletons (Stanton 1976; Schopf 1978) or because taphonomic processes preferentially destroy some that do (Powell *et al.* 1982). Comparison of the amount of prey consumed by preserved predators with the amount of prey species found in the assemblage permits an estimation of the minimum amount of biomass present at the next lower trophic level that was not preserved. Stanton and Nelson (1980) and Stanton *et al.* (1981) considered abundances, ecologic efficiencies, and total biovolumes of preserved species to make this estimation. Estimations based on energy flow, however, are superior. For example, we can deduce from Table 5 that at least 20 g of non-preserved annelidan prey had to be present to feed the individuals of *H. nodocarinatus*. This is a lifetime requirement, however, so that the 20 g of prey were not present at any one time. Probably, in fact, the predators also were not present simultaneously, because time-averaging affects the fossil assemblage. Trophic reconstructions in palaeoecology differ from those in ecology in that they encompass entire life spans and perhaps many generations, and do not imply simultaneous presence of all components in the community.

Ecologic efficiencies are commonly stated to be between 10 and 20% between higher trophic levels and to be generally lower between trophic levels one and two. Table 6 presents ecologic efficiencies as the ratio NP_n/NP_{n-1} where NP (net production) = $P_g + P_r$ (growth + respiration, although in most cases only P_g has been measured so that $NP = P_g$). Ecologic efficiencies average 7% between trophic levels one and two and 16% between levels two and three. If the ratio of net production to biomass is similar for the two trophic levels, then about five to twenty times more prey biomass than predator biomass should be present. Thus, because predators usually are larger than their prey, predators should be relatively rare in communities. Curiously, predatory gastropods are numerically dominant in the Stone City Formation, a fact that led Stanton and Nelson (1980) to use ecologic efficiency to estimate the amount of prey not preserved. Ecologic efficiencies, however, are based on data computed per area per year, whereas fossil assemblages must be treated on a per-lifetime basis. Therefore, the prey biomass that must be present to feed a predator is a function not only of their number and biomass, but also of the relative life spans of both predator and prey. If the predator lives

TABLE 6. Ecologic efficiency expressed as the ratio net production at one trophic level to the net production at the next lower trophic level (NP_n/NP_{n-1}).

Trophic levels	NP_n/NP_{n-1}	Comments	Source
1–2	0·021	—	Teal (1962)
2–3	0·064		
1–2	0·16		
2–3	0·05	—	Odum, H. T. (1957)
3–4	0·09		
1–2	0·11	—	Baird and Milne (1981)
2–3	0·28		
1–2	0·04	Los Maritas site—without meiofauna, benthos only, trophic level 2	Edwards, R. R. C. (1973)
2–3	0·21		
1–2	0·005	San Luis site—benthos only, trophic level 2	
2–3	0·20		
Avg. 1–2	0·07		
2–3	0·16		

significantly longer than the prey, then the total biomass of prey required to feed a given biomass of predator over the predator's life span must be higher than if their life spans were similar. Thus, predators should be very rare in fossil assemblages relative to their prey.

In the Stone City example, *P. aratus* consumed 11–15 g of prey to produce 3 g of biomass, an efficiency of 20–27%, and *N. texana* consumed 5–10 g of food to produce 1·3 g, an efficiency of 13–26%, but the much longer-liver *H. nodocarinatus* expended a much higher percentage of its energy in respiration, so that 20–30 g of prey were required to support 0·53 g of predator, an efficiency of only 2–3%. *H. nodocarinatus* has a poor palaeoecologic efficiency, not because the daily assimilation efficiencies were low, but because gross growth efficiency declines with age (Calow 1977). Older individuals, while consuming more, produce much less. For *H. nodocarinatus*, most of the energy flow of the population is contributed by a few older individuals.

Ecologic efficiencies, such as those in Table 6, are difficult to apply in palaeoecology because they are not based on the individuals' life spans. Thus, palaeoecologic efficiencies and the inferences made from them may be considerably different from their ecologic countertypes discussed by Kozlovsky (1968) and others.

Percent maximum age

Calculation of energy flow requires an age–size relationship for each species. If this cannot be established, a relationship between size and percent maximum age might be used. In this case the maximum size would be assigned an arbitrary age in equation 2. Two methods might be used. (1) All maximum sizes could be given the same age. Most molluscs have life spans in the range of one to twenty years, so an age of five years, for example, could be used. Table 5 shows the variability that results in data on energy flow even when realistic ages are used to bracket the real age. In cases where the age structure of the population includes individuals near maximum size, the discrepancies are large. For example, values for *N. texana* differ by 50%; for *H. nodocarinatus* and *P. aratus*, 33%, although the range of maximum ages used was about five years. Assigning each species the same maximum age rewards the short-lived species in the analysis and penalizes those long-lived species with good survivorship. (2) A value of $s_T = 1$ might be used so that the age determination is based on a single growth curve. This method rewards larger species regardless of their survivorship. Stanton *et al.* (1981) discussed the implications of this method (see fig. 14 in Stanton *et al.* 1981); using it, they predicted that *L. moorei* was the predominant predator in the Stone City assemblage. This is not the case (Table 5) because *L. moorei* never reached reproductive age. Neither of these two alternatives yields a realistic estimate of energy flow. Some species will be penalized, others rewarded, and often substantially so. There is no substitute for knowledge of the individual's actual age.

CONCLUSIONS

The interpretation of the community in palaeoecology has been largely based on taxonomic composition and relative abundance and on structural measures such as diversity and equitability. Reconstruction of the trophic relationships within the community may provide information about the environment as well as about the evolution of ecosystems through geologic time. Trophic reconstruction has been difficult, however, because abundance does not provide a satisfactory picture of the trophic importance of a species in the community.

This paper describes a simple procedure to resolve this problem by determining energy flow through each population. Consequently, the relative trophic importance of each species can be determined. In addition, non-preserved components of the trophic web can be included in the trophic reconstruction by estimating the amount of prey consumed by the preserved components. Analysis of the community in terms of energy flow brings into sharper focus the influence of taphonomy and time-averaging in determining the composition of the fossil assemblage. Their role in the formation of the fossil assemblage must be ascertained and evaluated if the trophic structure of a palaeo-community is to be viewed in the same terms as the trophic structure of an ecologic community.

We have described the steps necessary to determine energy flow within a fossil community. Before the procedure is applied in palaeoecology, the potential user must be convinced that the fossil assemblage provides a reasonable representation of the original community. We believe that in many, but not all, cases this is true and the analysis will provide useful information.

Two basic categories of data are necessary for the analysis: (1) size and age information for each population in the community, and (2) energy parameters, which are based on measurements from living organisms. We have pointed out sources of error in these two categories, and have also shown the effect differences in these input data will have on the final results. Improvement of the estimations in both categories is clearly desirable, but present uncertainties in them are small enough that their use can improve substantially trophic analysis of palaeo-communities.

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MAASTRICHTIAN NON-HETEROMORPH AMMONITES FROM THE MIRIA FORMATION, WESTERN AUSTRALIA

by R. A. HENDERSON *and* K. J. MCNAMARA

ABSTRACT. Twenty-two species of non-heteromorph ammonites, distributed among fourteen genera, are described from the Miria Formation, Western Australia. The species *Kitchinites spathi*, *Gunnarites raggatti*, *Kossmaticeras* (*Natalites*) *brunnschweileri*, *Neograhamites carnarvonensis*, and *Brahmaites* (*Brahmaites*) *kossmati*, and the subspecies *Pachydiscus* (*Pachydiscus*) *neubergicus dissitus* and *P.* (*P.*) *jacquoti australis* are described as new. *Pachydiscus* species shared with Western Europe date the Miria Formation as Maastrichtian, consistent with its age assignment based on Foraminifera. The Kossmaticeratidae is the most diverse family, contributing more than a third of the species. Maastrichtian records for the kossmaticeratid genera *Gunnarites*, *Maorites*, *Kossmaticeras* (*Natalites*), *Grossouvrites*, and *Neograhamites*, which previously had been thought to range no higher than Campanian, are new. The age attributable to the Miria Formation ammonite assemblage is reviewed in relation to standard Maastrichtian ammonite faunas from Western Europe.

THE Miria Formation (Miria Marl of Condon *et al.* 1956) occurs as a thin unit in the Cretaceous succession of the Giralia Anticline, which forms the Giralia Range, lying to the south of Exmouth Gulf, Western Australia. It consists of cream calcarenite 0·6–2·0 m thick, underlain by the Korojon Calcarenite and disconformably succeeded by the Palaeocene Boongerooda Greensand. Phosphatic grains and nodules are locally abundant and much of the rich fossil complement of the Miria Formation occurs as phosphatic moulds. Stream dissection of the western and north-eastern flanks of the Giralia Range provide the principal exposures of the Miria Formation. Here the unit is abundantly fossiliferous over a strike-length of about 80 km (text-fig. 1).

A rich fauna is present in the Miria Formation. In addition to ammonites, it includes a diverse assemblage of Foraminifera (Edgell 1957; Belford 1958), the nautiloid *Cimomia tenuicostata* Glenister, Miller and Furnish (1956) and a number of undescribed brachiopods, corals, echinoids, sponges, bryozoans, and shark teeth. Unpublished work by Darragh and Kendrick (pers. comm.) has revealed an assemblage of over sixty species of gastropods and bivalves.

The ammonites are especially noteworthy. Existing collections contain over 1500 specimens and constitute the most abundant assemblage of Maastrichtian ammonites as yet recorded. The assemblage is thus highly relevant to any assessment of the abundance and diversity of ammonites immediately prior to their demise at the end of the Cretaceous Period.

Early reports of the Miria Formation by Condit (1935) and Raggatt (1936) noted its fossiliferous nature and a collection of ammonites was examined by Whitehouse (*in* Raggatt 1936). A number of ammonites collected by C. Teichert in 1938 were described by Spath (1941), who recorded eight species of non-heteromorph ammonites: *Paraphylloceras* aff. *nera* (Forbes), *Phyllopachyceras forbesianum* (d'Orbigny), *Pseudophyllites* cf. *indra* (Forbes), *Hauericeras durga* (Forbes), *Kossmaticeras* sp. nov.? aff. *aemilianus* (Stoliczka), ?*Kitchinites* sp. indet., *Pachydiscus gollevillensis* (d'Orbigny), and *Pachydiscus* sp. nov.? cf. *grossouvrei* Kossmat. Spath, following Raggatt, erroneously described the ammonites as coming from 'glauconitic sand to sandstone'. The unit to which they refer is the overlying Boongerooda Greensand. This error no doubt arose from the way in which the ammonites occur, eroded out and scattered on the ground surface.

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Brunnschweiler (1966), in describing the heteromorph ammonite fauna of the Miria Formation, favoured a late Cretaceous age for the Boongerooda Greensand, on account of the rare occurrence of ammonites. We have also collected ammonites from the base of the Boongerooda Greensand, but they are often worn and invariably have glauconitic and phosphatic coatings. We regard them as having been reworked from the underlying Miria Formation. An early Palaeocene (planktonic Foraminiferal Zone 2) age attributed to the Boongerooda Greensand by McGowran (1968, 1978) supports this view and indicates a disconformable relationship between it and the Miria Formation.

Spath (1941) suggested an early Maastrichtian age for the ammonites he examined. Brunnschweiler (1966), however, considered that the heteromorph ammonite fauna was of late Campanian to early Maastrichtian age. The collection in recent years of a large number of specimens has allowed us to present this first embracing description of the non-heteromorph ammonites and to reassess the age of the fauna.

We will be revising the heteromorph ammonite fauna in a forthcoming paper. The descriptions are based primarily on three major collections: one made by G. Kendrick and T. Darragh in 1969, another by K.J.M. with Kendrick and Darragh in 1979, and the third by the same group plus R.A.H. in 1983. These collections are housed in the Western Australian Museum (WAM) and the Museum of Victoria (NMV). We have also made use of Teichert's 1938 collection, which is housed in the Department of Geology, University of Western Australia (UWA). Other specimens examined and referred to in the text are from collections in the British Museum, National History (BM), and the Oxford University Museum (OUM).

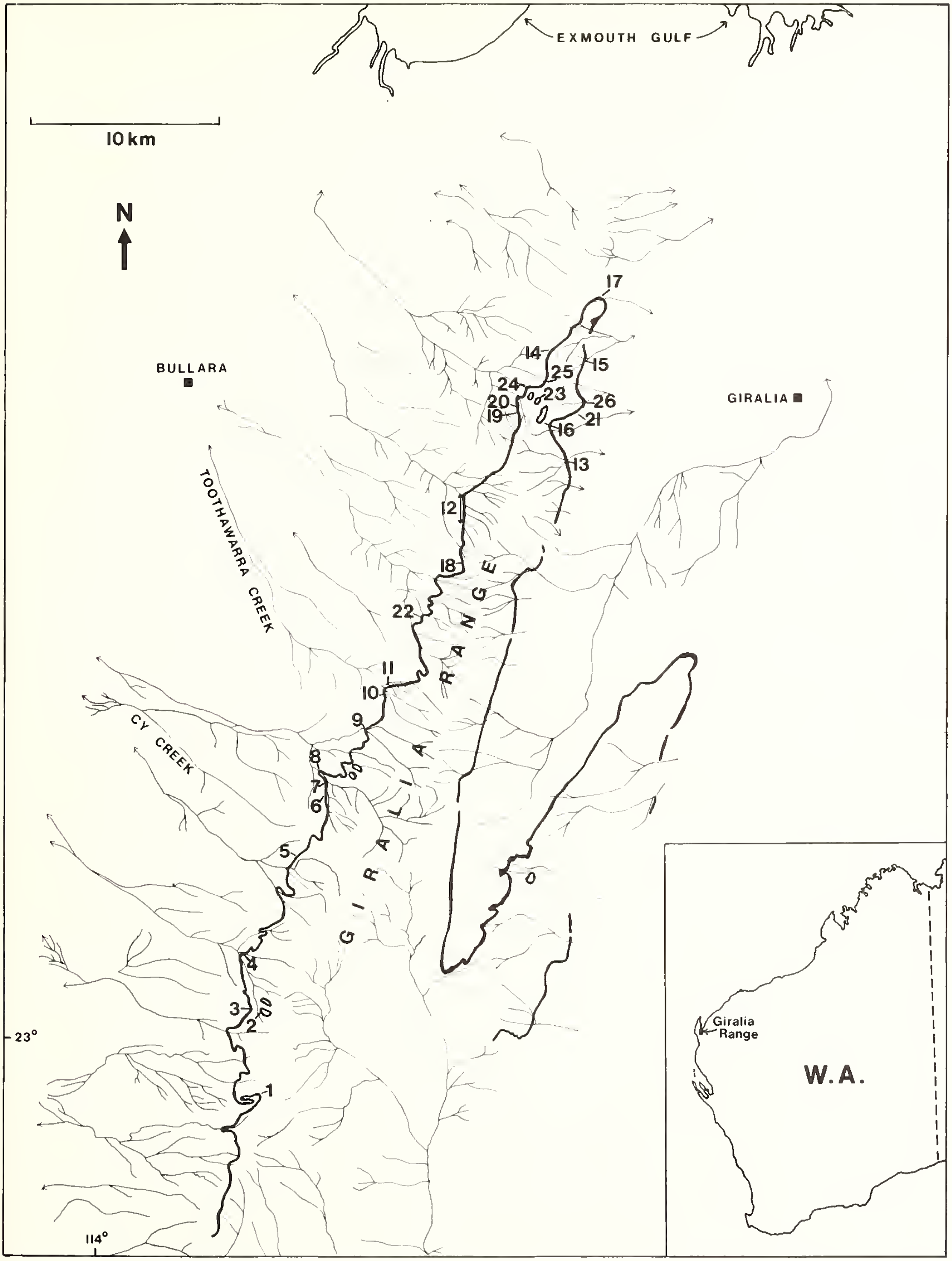
The positions of the twenty-six localities, which provided the collections on which this paper is based, are shown in text-fig. 1 and listed below.

1. Remarkable Hill, Cardabia Station (KV 013502). 2. Section Hill, Cardabia Station (KV 017543). 3. 500 m west of Section Hill, Cardabia Station (KV 012543). 4. 3·5 km north-north-west of Section Hill, Cardabia Station (JV 997579). 5. Creek, 6·5 km east of no. 10 bore, Cardabia Station (KV 026630). 6. Southern tributary of CY Creek, Cardabia Station (KV 044657). 7. CY Creek, Cardabia Station (KV 044667). 8. CY Creek, Cardabia Station, 2–3 km east of no. 37 bore (KV 038679). 9. Northern tributary of CY Creek, Cardabia Station (KV 070708). 10. Southern tributary of Toothawarra Creek, Cardabia Station (KV 069722). 11. Type section of the Miria Formation, Toothawarra Creek, Cardabia Station (KV 070725). 12. 3–6 km north-north-west of Whitlock Dam, Giralia Station (KV 115812–115832). 13. 7 km west-south-west of Deep Well, Giralia Station (KV 160832). 14. East side of Walatharra Paddock, Giralia Station (KV 169912). 15. 12 km west of Giralia Homestead, Giralia Station (KV 180910). 16. 2·3 km west-south-west of West Tank, Giralia Station (KV 160870). 17. 6 km south of Centipede Hill, Giralia Station (KV 180945). 18. 2 km west-north-west of Whitlock Dam, Giralia Station (KV 116789). 19. 4 km west-south-west of West Tank, Giralia Station (KV 143872). 20. 4 km west-north-west of West Tank, Giralia Station (KV 145880). 21. 1 km west-north-west of West Tank, Giralia Station (KV 174880). 22. 5 km west-south-west of Whitlock Dam, Bullara Station (KV 090770). 23. 2·5 km north-west of West Tank, Giralia Station (KV 159885). 24. 3·5 km north-west of West Tank, Giralia Station (KV 150890). 25. 3 km north-west of West Tank, Giralia Station (KV 160895). 26. 1 km north-west of West Tank, Giralia Station (KV 175883).

All grid references refer to the Giralia 1 : 100 000 topographic map, except for locality 1, which is on the adjacent Mia Mia 1 : 100 000 sheet.

SYSTEMATIC PALAEONTOLOGY

Morphological terms are from Arkell *et al.* (1957), except those applied to elements of the suture, which are from Wedekind (1916, see Kullman and Wiedmann 1970), and to the septal surface of the Lytoceratina, which are from Henderson (1984). Synonymy lists are selective and contain only important revisions, significant recent citations, and new additions. Dimensions are in millimetres and the following abbreviations are employed: D, shell diameter; H whorl height; B, whorl breadth; B/H, whorl breadth/height ratio; U, umbilical diameter; %, umbilical diameter as a percentage of the shell diameter.


EXMOUTH GULF
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BULLARA
GIRALIA
TOOTHAWARRA CREEK
CY CREEK
GIRALIA RANGE
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19
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21
22
23
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25
26
23°
114°
Giralia Range
W.A.

TEXT-FIG. 1. Locality map showing the distribution of the Miria Formation and the location of sites from which collections have been made. Outcrop data based on Condon *et al.* (1956).

Suborder PHYLLOCERATINA Arkell, 1950
Family PHYLLOCERATIDAE Zittel, 1884
Subfamily PHYLLOCERATINAE Zittel, 1884
Genus PHYLLOCERAS Suess, 1865
Subgenus NEOPHYLLOCERAS Shimizu, 1934

1934 *Neophylloceras* Shimizu, p. 61.
1935 *Paraphylloceras* Shimizu (*non* Salfield, 1919), p. 180.
1947 *Hyporbulites* Breistroffer, p. 82.
1956 *Epiphylloceras* Collignon, p. 24.

Type species. Ammonites (*Scaphites?*) *ramosus* Meek, 1857.

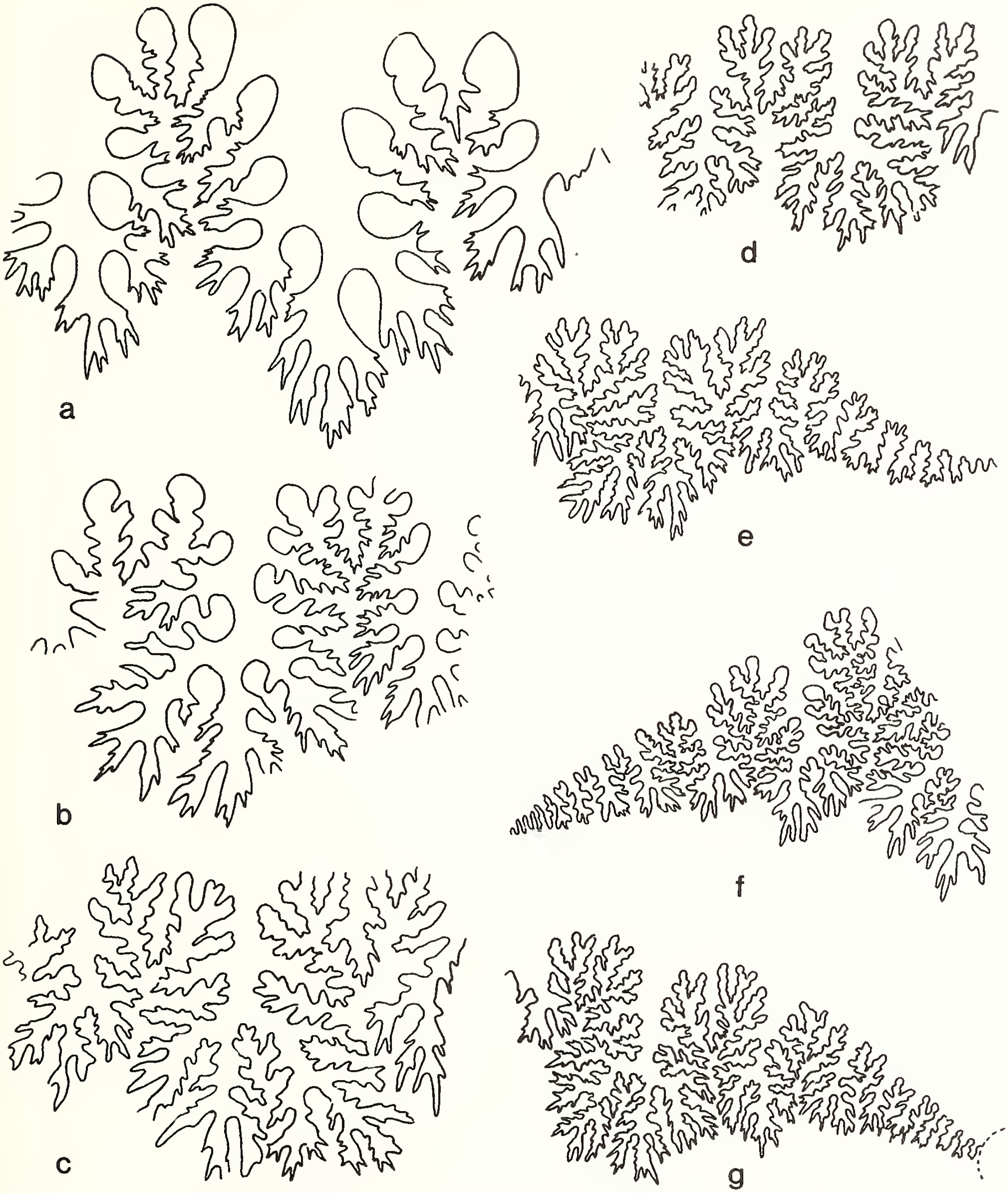
Diagnosis. Moderately to strongly compressed, strongly involute shells retaining a small open umbilicus and ornamented with thin, closely spaced, radial or weakly flexuous lirae. Additional ornament of radial costae, or indistinct, broad folds or narrow, shallow grooves may be present on the dorsal flanks. Suture complexly divided with small, indistinctly tetraphylloid terminations to saddles margining the lateral lobe.

Remarks. Neophylloceras was introduced by Shimizu (1934) in an obscure publication and was largely ignored until Wright and Matsumoto (1954) reviewed its status and confirmed its validity. Subsequently its usefulness has been much debated. It was treated as a junior subjective synonym of *Hypophylloceras* Salfeld, 1924 by Arkell, Kummel and Wright (1957), Wiedmann (1962*a*), Wiedmann and Dieni (1968), and Kennedy and Klinger (1977*a*). However, Usher (1952), Matsumoto (1959*a*, *b*), Packard (1960), Jones (1963), and Henderson (1970) all considered *Neophylloceras* as distinct by virtue of its more complex suture with less pronounced phylloid terminations to the saddles when compared with *Hypophylloceras*. Birkelund (1965) and Matsumoto and Morozumi (1980) thought that *Neophylloceras* was best placed as a subgenus of *Hypophylloceras*.

Wiedmann (1962*a*, *b*) drew attention to the very slow evolution of Jurassic and early Cretaceous *Phylloceras* and its Cretaceous derivative stocks whereby Jurasic representatives are separated from those of late Cretaceous age by rather small morphological differences. This had resulted in the introduction of a plethora of generic categories into the literature to represent very small changes in morphology, for reasons of biostratigraphic propriety rather than those of objective systematics.

The only characteristic which serves to distinguish Jurassic *Phylloceras* from their Cretaceous descendants is the nature of the suture. It is relatively simple, with large biphylloid or triphylloid terminal elements to the saddles in Jurassic species, of which the type species *P. heterophyllum* (Sowerby) is a typical representative, and becomes much more complex with small, almost unrecognizable, tetraphylloid terminations to the saddles in late Cretaceous forms (text-fig. 2). When the complete array of species is considered, all gradations in sutural type are evident (text-fig. 2) and natural breaks in the range of morphology are not readily apparent.

There are, however, three clusters of species which may be recognized on the basis of sutural morphology and into which the great majority of species can be readily fitted. Generic categories are already well established for all three: *Phylloceras* Suess (*s.s.*), type species *P. heterophyllum* (Sowerby); *Hypophylloceras* Salfeld, type species *H. onoense* (Stanton); and *Neophylloceras* Shimizu, type species *N. ramosum* (Meek). Even though the two end-members, *Phylloceras* (*s.s.*) and *Neophylloceras*, are quite separate in sutural character, subgeneric status is here considered to be the most satisfactory way of expressing relationships within the *Phylloceras* (*s.s.*)-*Hypophylloceras*-*Neophylloceras* plexus. Following Matsumoto (1959*a*) *P. seresitense* Pervinquière, which is intermediate between *P.* (*H.*) *onoense* and *P.* (*N.*) *ramosum* in terms of its suture, is included in *Neophylloceras*. *Hyporbulites* Breistroffer, with *P.* (*N.*) *seresitense* as its type species, thereby becomes a junior subjective synonym of *Neophylloceras*.



TEXT-FIG. 2. *a–c*, sutural discrimination of subgenera within *Phylloceras*. *a*, type species of *Phylloceras* (*Phylloceras*), *P.* (*P.*) *heterophyllum* (J. Sowerby), OUM J17844, Toarcian, × 1½; *b*, type species of *Phylloceras* (*Hypophylloceras*), *P.* (*H.*) *onoense* (Stanton), from Matsumoto 1959*a*, text-fig. 5, lower Cretaceous (precise age uncertain), × 1½; *c*, type species of *Phylloceras* (*Neophylloceras*), *P.* (*N.*) *ramosum* (Meek), from Jones 1965, text-fig. 7, upper Campanian or lower Maastrichtian, × 1½. *d–g*, sutures of *Phylloceras* (*Neophylloceras*). *d*, *P.* (*N.*) *seresitense* (Pervinquiere) from Matsumoto 1959*a*, text-fig. 3, upper Albian or Cenomanian, × 3; *e*, *P.* (*N.*) *hetonaiense* Matsumoto, from Jones 1963, text-fig. 8, upper Campanian or lower Maastrichtian, × 1·25; *f*, *P.* (*N.*) *groenlandicum* Birkelund, from Birkelund 1965, text-fig. 8, Maastrichtian, × 3·5; *g*, *P.* (*N.*) *surya* (Forbes), WAM 81.2409, lower Maastrichtian, × 2·5.

Phylloceras (Neophylloceras) as thus defined ranges from the Albian to the Maastrichtian and includes some twenty nominate species among which there are doubtless a substantial number of synonyms. *Epiphylloceras* Collignon 1956 (type species *Ammonites surya* Forbes) has been consistently treated as a synonym of *Neophylloceras*. *Paraphylloceras* Shimizu 1935, also introduced for *A. surya* Forbes and its allies, is a stillborn homonym of *Paraphylloceras* Salfeld 1919 (see Wright and Matsumoto 1954). *A. surya* is redescribed herein and the widely held view that it is best considered a *Neophylloceras* is re-endorsed.

Phylloceras (*Neophylloceras*) *ramosum* (Meek, 1857)

Plate 1, figs. 1–3; text-fig. 2*c*

1857 *Ammonites* (*Scaphites?*) *ramosus* Meek, p. 45.
1970 *Neophylloceras ramosum* (Meek); Henderson, p. 5, pl. 1; fig. 3, text-fig. 2*a*.
1980 *Hypophylloceras ramosum* (Meek); Blasco *et al*., p. 477, pl. 2, figs. 1–4.

Material. Four specimens, localities 12, 15, 18, and 23.

Description. Shell discoidal and strongly involute, the umbilicus measuring some 8·5% of the shell diameter. Whorls approximately twice as wide as high, very weakly convex, their axis of maximum width a little dorsal of the mid-flank. Umbilical wall steep, curving smoothly into the flank, without an abrupt shoulder. Flanks only very slightly convergent so that the venter is quite broadly arched for such a compressed shell. Ornament of fine, closely spaced lirae numbering approximately 125–150 in a half whorl, becoming slightly more numerous with growth. Lirae are not preserved on the dorsal flanks; they are rectiradiate on the ventral flanks and weakly projected across the venter. Suture complexly divided with auxiliary elements of the umbilical lobe arrayed in a radial line.

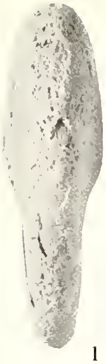
Dimensions.

	D	H	B	B/H	U	%
WAM 80·968	41·0	23·5	12·0	0·51	3·5	9

Remarks. *P.* (*N.*) *ramosum* is widely distributed on the borderlands of the Pacific Ocean, having been recorded from Alaska, Vancouver Island, California, southern South America, the Antarctic Peninsula, New Zealand, and Japan. However, nowhere is it represented by a substantial suite of specimens allowing proper documentation of its intraspecific variation. In consequence, its relationships to other nominate species of *Phylloceras* (*Neophylloceras*) are somewhat conjectural. It is closely related to *P.* (*N.*) *hetonaiense* Matsumoto (redescribed by Matsumoto 1959*b* and Jones 1963) (= *P.* (*N.*) *lambertense* Usher, 1952) and to *P.* (*N.*) *woodi* (van Hoepen, 1921) (redescribed by Kennedy and Klinger 1977*a*) (= *Hyporbulites hoepeni* Collignon, 1956). A distinction from these two species appears to be provided by its more compressed whorl profile, at least in the early growth stages to a shell diameter of some 50 mm, and by more flexuous lirae. Its distinction from the Indian *P.* (*N.*) *nera* (Forbes) is less convincing and depends solely on the lirae which are less flexuous in the Indian species and not projected on the venter.

EXPLANATION OF PLATE 1

Figs. 1–3. *Phylloceras* (*Neophylloceras*) *ramosum* (Meek), WAM 80.968, × 1.
Figs. 4–6. *Partschiceras* (*Phyllopachyceras*) *forbesianum* (d'Orbigny), WAM 80.965, × 1.
Figs. 7–8, 11–12. *Phylloceras* (*Neophylloceras*) *surya* (Forbes). 7–8, NMV P31021. 11–12, WAM 82.3081, × 1.
Figs. 9–10. *Anagaudryceras politissimum* (Kossmat), WAM 80.986, × 1.
Figs. 13–14. *Gaudryceras kayei* (Forbes), WAM 80.989, × 1.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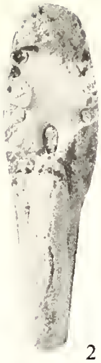
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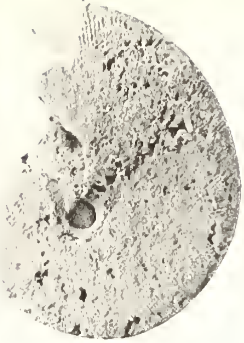
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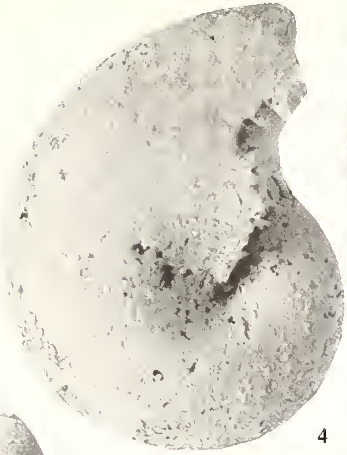
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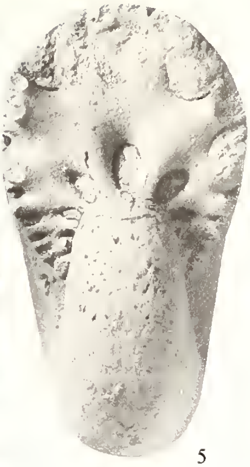
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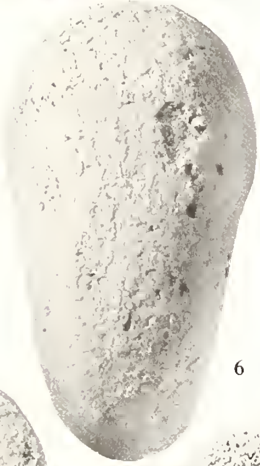
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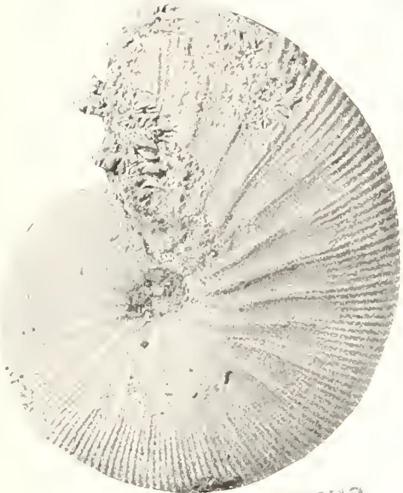
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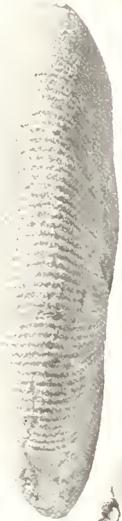
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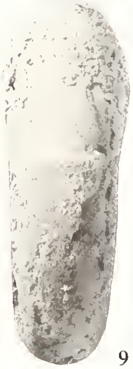
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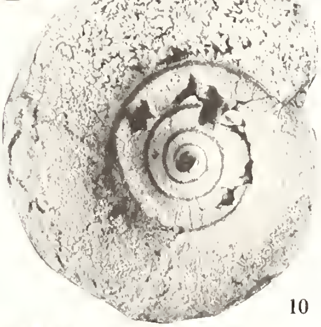
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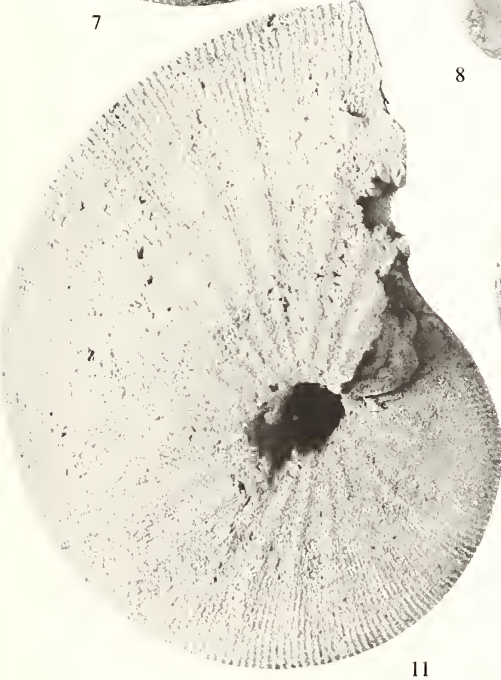
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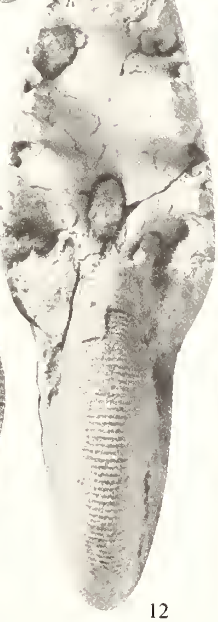
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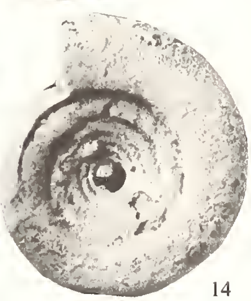

14

HENDERSON and McNAMARA, Phylloceratidae and Gaudryceratidae

Phylloceras (*Neophylloceras*) *surya* (Forbes, 1846)

Plate 1, figs. 7, 8, 11, 12; Plate 2, figs. 1, 2; text-fig. 2*g*

1846 *Ammonites surya* Forbes, p. 106, pl. 7, fig. 10*a*, *b*.
1941 *Paraphylloceras* sp. cf. *nera* (Forbes); Spath, p. 42.
1956 *Epiphylloceras mikobokense* Collignon, p. 24, pl. 2, fig. 3, 3*a*; pl. 4, fig. 5, 5*a*, *b*.
1971 *Epiphylloceras mikobokense* Collignon; Collignon, p. 1, pl. 640, fig. 2359.
1971 *Epiphylloceras geczyi* Collignon, p. 1, pl. 640, fig. 2360.
1977*a* Phylloceras (Hypophylloceras) mikobokense (Collignon); Kennedy and Klinger, p. 368, pl. 12, fig. 1*a*, *b*.

Material. Forty-two specimens, localities 4–7, 9–13, 15–20, and 25.

Description. Shell discoidal and involute with an umbilicus measuring 8–11 % of the shell diameter. Whorls compressed, about twice as high as wide. Umbilical wall vertical at the umbilical seam but curves outward, passing smoothly across the umbilical shoulder into the flanks which are weakly convex and converge to a narrowly rounded venter. Axis of maximum whorl breadth lies on the dorsal flanks, close to the umbilical shoulder. Ornament is of two orders. Fine, closely spaced striae separated by interspaces as wide as themselves, begin on the dorsal flanks. They are initially prorsiradiate but straighten in the mid-flank region to become almost rectiradiate. On some shells they curve slightly forward again across the venter and are thus rendered very weakly flexuous, but on others they pass straight across the venter. Striae number some sixty-five to eighty-eight per half whorl on shells 40–60 mm in diameter, but become more closely spaced relative to the shell diameter with growth so that large shells about 120 mm in diameter have 115–135 striae on the last half whorl. Well-spaced costae number twelve to fifteen per half whorl, many beginning from the umbilical shoulder, others intercalated on the dorsal flanks, reaching to the edge of the venter or almost so. On some shells they are distinctly prorsiradiate on the dorsal flanks, becoming rectiradiate in the mid-flank region; on others they are straight and rectiradiate or slightly prorsiradiate throughout. Suture very finely dissected with auxiliary elements of the umbilical lobe arrayed in a rectiradiate line.

Dimensions.

	D	H	B	B/H	U	%
Lectotype: BM C51075	36·5	20·0	11·0	0·55	3·5	10
NMV P31021	61·5	33·0	17·5	0·53	7·0	11
WAM 80.780	118·0	66·0	35·0	0·53	11·0	9

Remarks. Even though the Western Australian specimens consist mainly of whorl fragments, they are sufficient to show that the ornament is quite variable. Shells at the same growth stage show different densities of striation and strengths of costation; in addition, the curvature of both orders of ribs differs noticeably between specimens.

Six specimens of *P.* (*N.*) *surya* from Pondicherry, Southern India, including Forbes's type series, are held by the British Museum (Natural History). BM C51075 was figured by Forbes (1846, pl. 7, fig. 10*a*, *b*) and C51074 by Kossmat (1895, pl. 16, fig. 1*a*–*c*). They likewise show the ornament to be variable. The largest specimen, that figured by Kossmat, has some ninety-five striae on the last half whorl at a shell diameter of some 120 mm. It is thus more sparsely striate than any of the Western Australian specimens of comparable size. Two smaller specimens, with shell diameters of about 40 mm, have some fifty-five and sixty-five striae respectively, on their last half whorls, overlapping with the western Australian suite in this characteristic.

P. (*N.*) *mikobokense* (Collignon, 1956) lies within the range of variation of *P.* (*N.*) *surya* and is synonymous with it. *P.* (*N.*) *geczyi* (Collignon, 1971) is also considered to be a junior synonym. It was differentiated because of its more flexuous striae and sparse, irregular costae. Its striation appears to fall within the range of variation shown by the Pondicherry suite in the British Museum (Natural History) and by Western Australian *P.* (*N.*) *surya*. Its costation does not differ greatly from that shown by the specimen of *P.* (*N.*) *surya* figured by Stoliczka (1865, p. 115, pl. 58, fig. 5).

Two other species have ornament comparable with that of *P.* (*N.*) *surya*. They are *P.* (*N.*) *radiatum* (Marshall, 1926, p. 135, pl. 19, fig. 6; pl. 26, figs. 3, 4) which is of doubtful status because its type series has been lost (Henderson 1970, p. 6), and *P.* (*N.*) *cottreaui* (Collignon, 1956, p. 25, pl. 4, fig. 6, 6*a*). Both of these species differ from *P.* (*N.*) *surya* in having more inflated whorls and *P.* (*N.*) *cottreaui* has, in addition, a much wider umbilicus.

Genus PARTSCHICERAS Fucini, 1920
Subgenus PHYLLOPACHYCERAS Spath, 1927

1927 *Phyllopachyceras* Spath, p. 36

Type species. Ammonites infundibulum d'Orbigny, 1841.

Diagnosis. Phylloceratidae with inflated whorls varying from somewhat compressed with an oval profile to equidimensional with a rounded profile. Umbilicus a minute pit measuring 4% or less of the shell diameter. Post-juvenile shell with broad ribs continuous across the venter. Suture with L and E of equal depth or nearly so.

Remarks. Phyllopachyceras Spath (1927) was introduced without a clear diagnosis but has been adopted by many authors (Roman 1938; Drushchits 1956; Arkell, Kummel and Wright 1957; Jones 1963) to include inflated, very narrowly umbilicate phylloceratids with coarse ribs appearing on post-juvenile growth stages. Such forms were considered to be exclusively of Cretaceous age. The type species of *Phyllopachyceras*, the Barremian *P. infundibulum* (d'Orbigny), has a whorl breadth/whorl height ratio of 0·65–0·88 (Wiedmann 1964, p. 241) and is perhaps the most compressed member of the group.

Wiedmann (1964) regarded *Phyllopachyceras* as a junior subjective synonym of the Jurassic genus *Partschiceras* Fucini (1920, p. 95) on the basis that species of these two taxa form a morphological continuum. However, the type species of *Partschiceras*, subsequently designated as *P. partschi* Stur by Spath (1927, p. 38), differs from *Phyllopachyceras infundibulum* and its allies in several characteristics. It has been described by a number of authors (see Kovacs 1942 for a synonymy listing) and has a compressed whorl profile (B/H 0·5–0·63) with rather flattened flanks, an umbilicus which measures 8–14% of the shell diameter, and conspicuous constrictions on its juvenile shell. In addition, its suture has L much deeper than E. Indeed *Partschiceras* differs from *Phylloceras* (*s.l.*) only in post-juvenile ornament and was introduced as a subgenus of *Phylloceras* by Fucini (1920), a view which has been followed subsequently by some authors (Kovacs 1942; Sturani 1966).

Phyllopachyceras is here provisionally regarded as a subgenus of *Partschiceras* (*s.l.*), its members distinguished by the relative depth of the external lobe of the suture (text-fig. 3) and the possession of a minute umbilicus. A more compressed whorl profile serves to distinguish many *Partischiceras* (*s.s.*) from *Phyllopachyceras* but there is overlap in this characteristic. The oldest *Phyllopachyceras* is considered to be the Valanginian species *P. rogersi* (Kitchin, 1908, p. 179, pl. 8, fig. 19, 19*a–c*; see also Collignon 1962, p. 20, pl. 181, figs. 815, 816 and Cooper 1981, p. 155) which has an external lobe of characteristic form but a much wider umbilicus than typical of the subgenus. The youngest is *P.* (*P.*) *forbesianum* (d'Orbigny) which ranges into the Maastrichtian in Western Australia and elsewhere. In all, the subgenus includes some nineteen species. *Partschiceras* (*s.s.*) is restricted to the Jurassic.

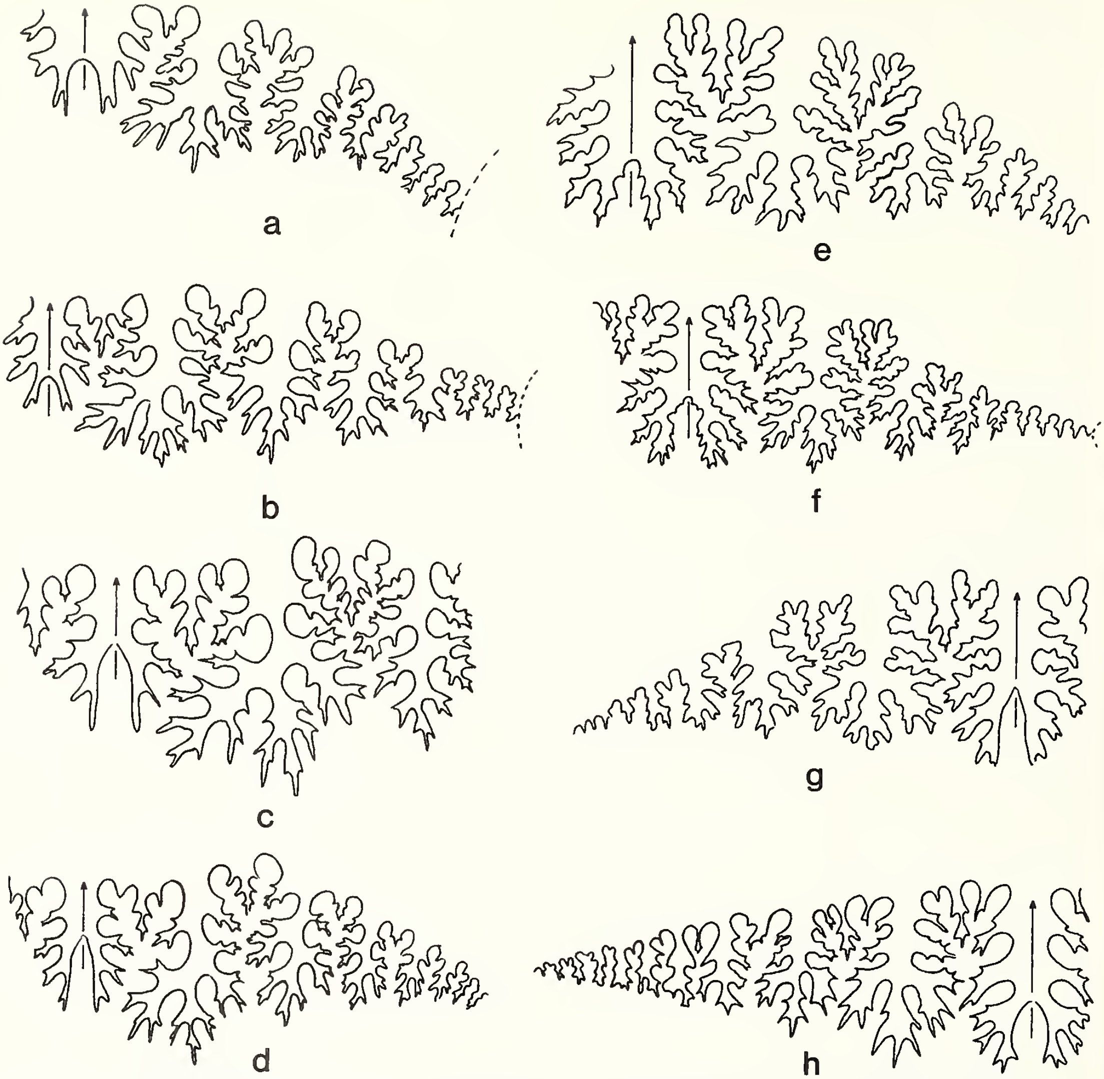
Partschiceras (*Phyllopachyceras*) *forbesianum* (d'Orbigny, 1850)

Plate 1, figs. 4–6; text-fig. 3*f*

1846 *Ammonites rouyanus* d'Orbigny; Forbes, p. 108, pl. 8, fig. 6.
1850 *Ammonites forbesianum* d'Orbigny, p. 213.
1970 *Phyllopachyceras forbesianum* (d'Orbigny); Henderson, p. 7, pl. 1, figs. 2, 4, 5.

Material. Forty-nine specimens, localities 3, 4, 6, 8–12, 15–20, 22, and 25.

Description. Shell involute, expanding rapidly, the umbilicus measuring 3–4% of the shell diameter. Umbilical wall steep, sloping outwards, umbilical shoulder not clearly demarcated. Whorls equidimensional with well



TEXT-FIG. 3. Discrimination of *Partschiceras* (*Partschiceras*) and *Partschiceras* (*Phyllopachyceras*) by means of the external lobe of the suture. *a–d*, *Partschiceras* (*Partschiceras*). *a*, the type species of *Partschiceras* (*Partschiceras*), *P.* (*P.*) *partschi* (Stur), from Geyer 1893, pl. 5, fig. 9, middle Liassic, ×6; *b*, *P.* (*P.*) *reptroplicatum* (Geyer), from Geyer 1893, pl. 6, fig. 3*c*, middle Liassic, ×3; *c*, *P.* (*P.*) *subobtusum* (Kudernatsch), from Sturani 1966, pl. 5, fig. 3, lower Bathonian, ×3; *d*, *P.* (*P.*) *viator* (d'Orbigny), from Sturani 1966, pl. 5, fig. 1, upper Bathonian, ×3. *e–h*, *Partschiceras* (*Phyllopachyceras*). *e*, *P.* (*P.*) *eichwaldi occidentale* Wiedmann, from Wiedmann 1964, text-fig. 55, Barremian, ×3; *f*, *P.* (*P.*) *forbesianum* (d'Orbigny), WAM 71.211b, lower Maastrichtian, ×2·5; *g*, the type species of *Partschiceras* (*Phyllopachyceras*), *P.* (*P.*) *infundibulum* (d'Orbigny), from Drushchits 1956, text-fig. 552, ×3; *h*, *P.* (*P.*) *rouyanum* (d'Orbigny), from d'Orbigny 1841, pl. 110, fig. 5, Neocomian, ?×1½.

arched flanks and venter. Ornament of fine lirae, rursiradiate on the umbilical shoulder and rectiradiate on the flanks and venter for all growth stages. Broad, weak, rather closely spaced folds appear at a shell diameter of about 35 mm. Suture complex with small phylloid terminations on the major saddles; ten auxiliary saddles in the umbilical lobe arranged in a rectiradiate line.

Dimensions.

	D	H	B	B/H	U	%
Lectotype BM C51081	31·5	17·8	18·0	1·01	0·8	3
WAM 60.52b	35·0	18·0	18·0	1·00	1·25	4
WAM 80.835	41·0	24·0	23·5	0·98	1·25	3
WAM 71.2116	46·0	27·0	26·0	0·96	2·0	4
WAM 80.985	48·5	26·5	28·5	0·93	2·0	4
WAM 86·965	56·0	34·0	32·0	0·94	2·0	4

Remarks. P. (*P.*) *forbesianum* is a long-ranging species, first appearing in the lower Santonian of Madagascar (Collignon 1966) and extending into the lower Maastrichtian in Western Australia and India.

Suborder LYTOCERATINA Hyatt, 1899
Superfamily TETRAGONITACEAE Hyatt, 1900
Family GAUDRYCERATIDAE Spath, 1927
Genus ANAGAUDRYCERAS Shimizu, 1934

Type species. Ammonites sacya Forbes, 1846 (= *A. buddha* Forbes, 1846).

Remarks. The status and content of *Anagaudryceras* has recently been reviewed by Kennedy and Klinger (1979). It is a widely distributed genus with very conservative morphological trends. Individual species typically show marked ontogenetic change, juveniles tending to be widely umbilicate with depressed whorls ornamented with fine lirae. Adults are generally more narrowly umbilicate with less depressed or even compressed whorls and commonly bear broad weak ribs in addition to lirae. Most species are known from no more than a few specimens which are often insufficient to properly characterize ontogenetic changes and intraspecific variation. In consequence, there is a plethora of poorly characterized *Anagaudryceras* species in the literature, including the type species *Ammonites sacya* (Forbes) which has been considered synonymous with *A. buddha* (Forbes) by a number of authors. Contrary to the view of Kennedy and Klinger (1979), *A. sacya* is the senior synonym, having been designated as such by Stoliczka (1865).

Anagaudryceras subtilineatum (Kossmat, 1895)

Plate 2, figs. 3, 4; text-fig. 4*a*

1895 *Lytoceras* (*Gaudryceras*) *subtilineatum* Kossmat, p. 123, pl. 19 figs. 1*a–c*, ?2*a*, *b*.
1979 *Anagaudryceras subtilineatum* (Kossmat); Kennedy and Klinger, p. 155, pl. 14, figs. 3, 12; text-fig. 3.

Material. Three specimens, localities 4, 23, and 24.

Description. Early growth stages, up to a shell diameter of about 35 mm, have strongly depressed volutions (B/H ratio of about 1·6) with strongly convex flanks scarcely discriminated from the convex, outwardly sloping umbilical wall and broadly arched venter. Umbilical diameter is about half the shell diameter. Later growth stages, up to 45 mm, are a little less evolute and the whorls become much less depressed with less strongly convex flanks, a more clearly marked umbilical shoulder, and more narrowly arched venter. Ornament consists of very fine lirae and infrequent, weak constrictions each of which is preceded by a prominent collar. Constrictions are weakly prorsiradiate on the umbilical wall, swing more strongly forward on the dorsal flanks, straighten slightly on the ventral flanks, and swing forward again across the venter. As far as can be seen the lirae follow the same course. Suture typical of the genus with L bifid and U retracted on the umbilical wall and subdivided into numerous auxiliary elements. External saddle finely and evenly serrated.

Dimensions.

	D	H	B	B/H	U	%
WAM 83.2721	36·5	10·0	14·8	1·48	17·2	47
WAM 81.2347	24·0	6·8	11·0	1·62	12·2	51
WAM 81.2347	*c.* 45·5	15·2	18·8	1·23	20·5	*c.* 45

Remarks. The figured Western Australian specimen (Pl. 2, figs. 3, 4) matches, almost exactly, the larger of Kossmat's two specimens which Kennedy and Klinger (1979) designated as lectotype. Kossmat's smaller syntype has a somewhat less depressed whorl section (B/H ratio of 1·4 at a shell diameter of 15 mm) and its specific identity is questionable.

Anagaudryceras politissimum (Kossmat, 1895)

Plate 1, figs. 9–10; text-fig. 4*d*

1895 *Lytoceras* (*Gaudryceras*) *politissimum* Kossmat, p. 128, pl. 15, fig. 7*a–c*.
1979 *Anagaudryceras politissimum* (Kossmat); Kennedy and Klinger, p. 154, pl. 5, fig. 3.

Material. Nine specimens, localities 6, 12, 16, 17, 20, 22, and 23.

Description. Early growth stages, up to a shell diameter of 35–40 mm, have slightly depressed volutions and are evolute. Later growth stages become increasingly compressed and are slightly more narrowly umbilicate. Volutions subcircular in section with convex flanks which pass smoothly into an outward sloping, convex umbilical wall; venter broadly rounded. Ornament consists of dense, fine lirae and some four prominent collars per whorl, each followed by a weak constriction. These elements are parallel and follow a slightly sinuous course, being markedly prorsiradiate on the dorsal flanks and venter, but slightly less so on the umbilical wall and ventral flanks. Suture typical of the genus with a lanceolate external saddle, L bifid and U retracted on the umbilical wall, with numerous auxiliary elements.

Dimensions.

	D	H	B	B/H	U	%
WAM 83.2716	29·0	9·5	11·0	1·16	12·5	43
WAM 83.2714	47·5	17·5	16·5	0·94	19·2	40
WAM 83.2715	52·0	17·5	16·5	0·96	20·0	38
WAM 83.2720	114·0	47·0	42·5	0·90	42·0	36

Remarks. The largest Western Australian specimen is still septate at a shell diameter of 114 mm so that fully grown complete shells must have exceeded 150 mm in diameter. *A. politissimum* was a long-ranging (Turonian–Maastrichtian) inhabitant of the Indian Ocean.

Genus GAUDRYCERAS de Grossouvre, 1894
Gaudryceras kayei (Forbes, 1846)

Plate 1, figs. 13, 14; Plate 2, figs. 5, 6, 9, 10; text-fig. 4*b*, *c*

1846 *Ammonites kayei* Forbes, p. 101, pl. 8, fig. 3*a*, *b*.
1979 *Vertebrites kayei* (Forbes); Kennedy and Klinger, p. 160, pl. 14, fig. 2*a–c*; text-fig. 5.

Material. Twenty-two specimens, localities 5, 6, 12, 14–17, 20–22, and 25.

Description. Early whorls, to a shell diameter of some 50 mm, are depressed with a broad venter; they expand slowly and embrace only slightly so that the umbilicus exceeds 50 % of the shell diameter. Later volutions are less depressed, becoming equidimensional at a shell diameter of some 75 mm, and have a more narrowly arched venter. They expand more rapidly and embrace more than the early volutions so that the umbilicus becomes narrower, representing 46 % of the shell diameter on the largest measurable specimen available. Thin, sharp, wire-like lirae swing forward on the umbilical wall, straightening on the flanks where they split into very fine

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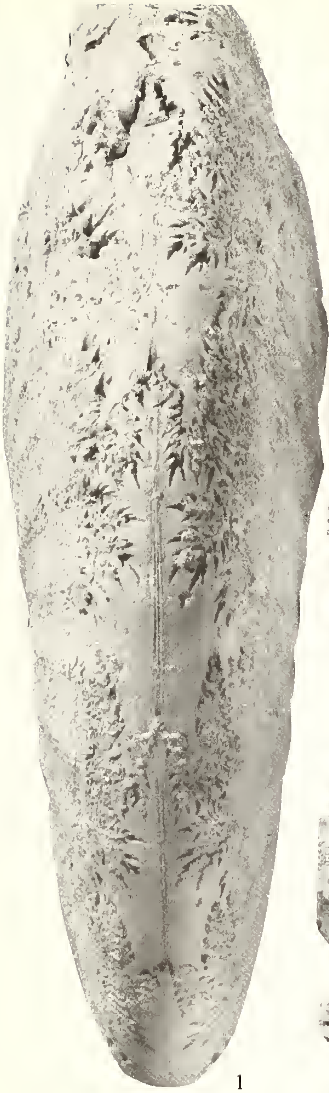
EXPLANATION OF PLATE 2

Figs. 1–2. *Phylloceras* (*Neophylloceras*) *surya* (Forbes), WAM 60.50, × 1.
Figs. 3–4. *Anagaudryceras subtilineatum* (Kossmat), WAM 81.2347, × 1.
Figs. 5–6, 9–10. *Gaudryceras kayei* (Forbes). 5–6, WAM 80.1002, × 1. 9–10, WAM 80.977, × 1.
Figs. 7–8. *Pseudophyllites indra* (Forbes), WAM 60.92d, × 1.

PLATE 2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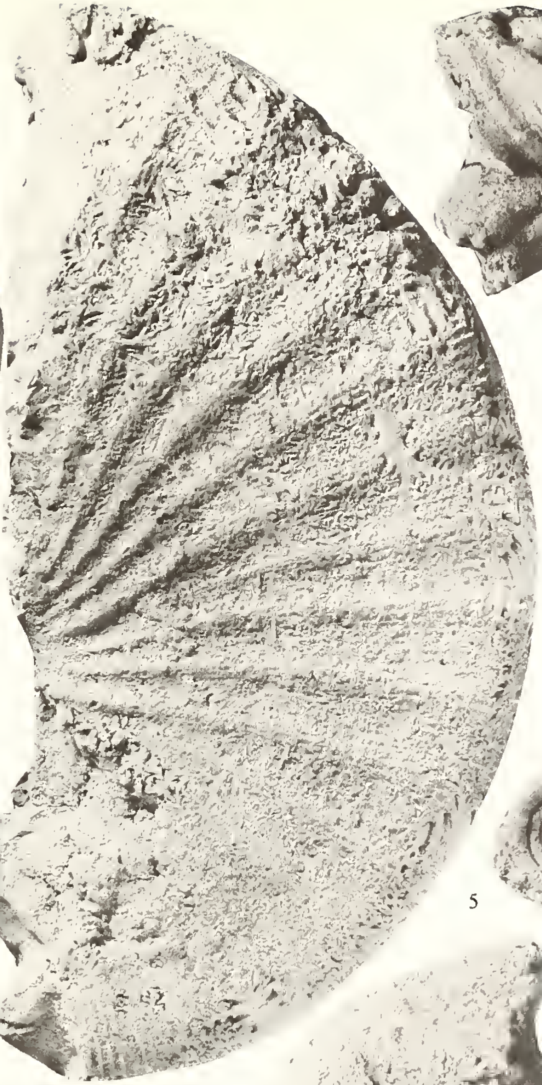
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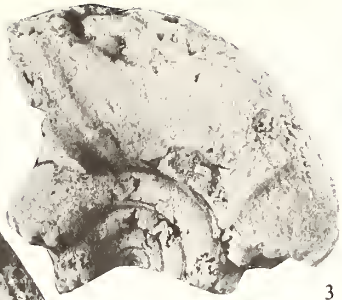
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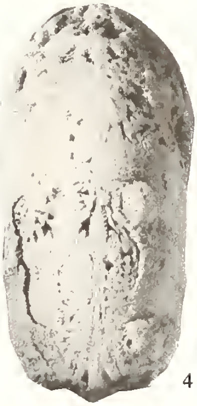
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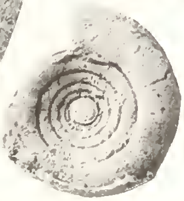
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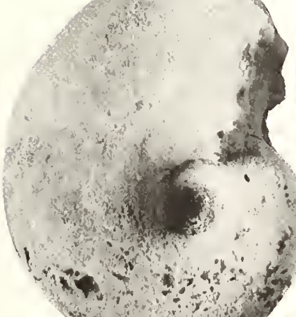
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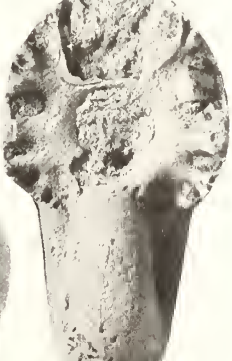
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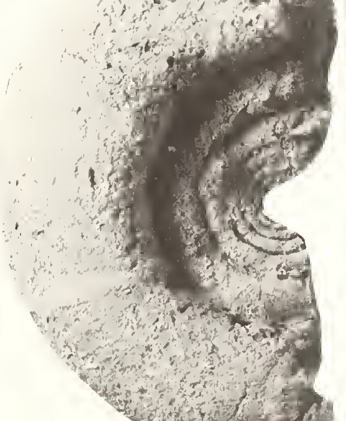
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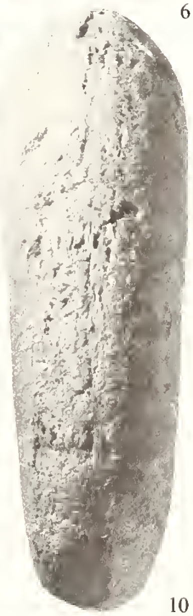
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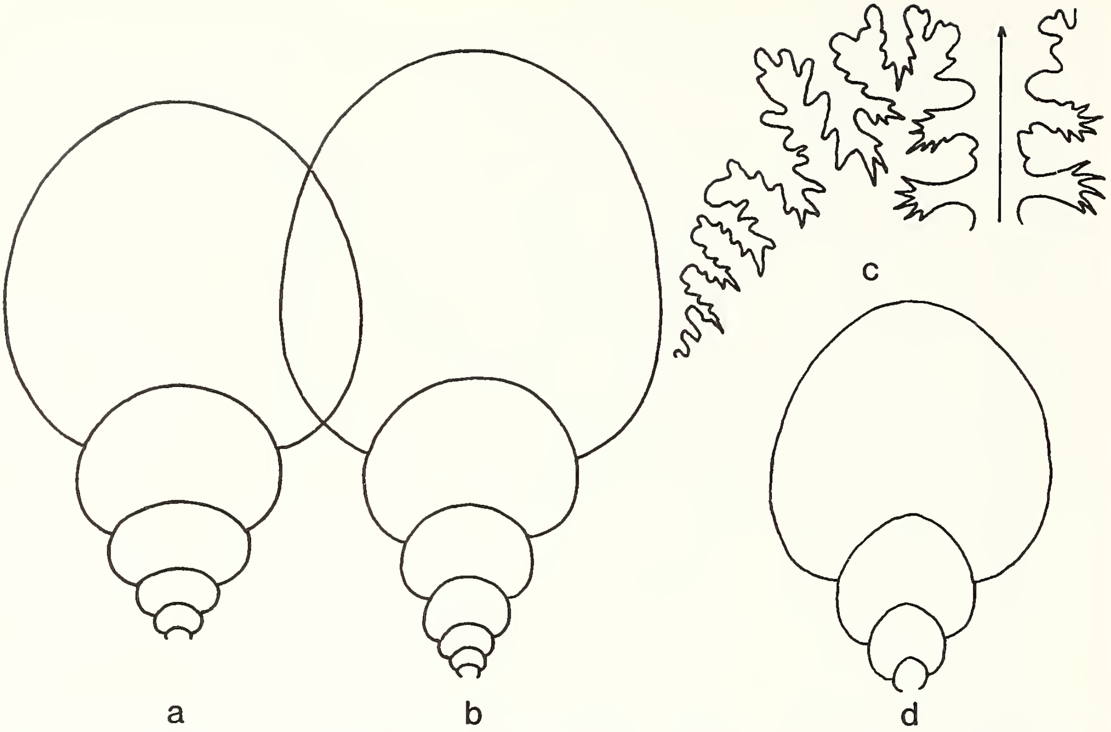
HENDERSON and McNAMARA, Phylloceratidae, Gaudryceratidae, and Tetragonitidae



TEXT-FIG. 4. *a*, whorl profile of *Anagaudryceras subtilineatum* (Kossmat), WAM 81.2347, × 2. *b*, whorl profile of *Gaudryceras kayei* (Forbes), WAM 80.977, × 2. *c*, internal suture of *G. kayei* (Forbes), WAM 80.839, × 8. *d*, whorl profile of *A. politissimum* (Kossmat), WAM 81.2698, × 2.

subdivisions which are weakly projected on the venter. Suture florid with the external saddle lanceolate, L bifid, and U deeply embayed with some fifteen auxiliary lobes.

Dimensions.

	D	H	B	B/H	U	%
WAM 80.1002	26·0	5·5	7·8	1·42	15·2	58
Lectotype: BM C51050	32·2	7·2	10·5	1·46	17·0	53
WAM 80.989	36·5	9·2	12·2	1·32	20·0	55
Syntype: BM C82498	36·5	9·2	12·0	1·30	18·2	50
WAM 82·3084	41·2	11·2	13·2	1·18	21·0	51
WAM 81.2611	55·0	17·0	19·0	1·12	26·5	47
Syntype: BM C51049	55·2	14·6	17·4	1·19	26·2	46
WAM 80.977	76·5	25·2	25·2	1·00	—	—
WAM 83·2701	—	47·0	44·8	0·95	—	—

Remarks. Ornamentation of the inner whorls, up to a shell diameter of 3 mm, shows on WAM 80.1002. Here the lirae are crowded together and the first whorl shows some fifteen regularly spaced stronger lirae, presumably marking constrictions. Later whorls have four to seven constrictions which are clear on internal moulds but faintly inscribed, or obscure, where the test is retained. Their primary lirae are separated by wide interspaces on the flanks, much wider than the lirae themselves.

G. kayei has been generally referred to *Vertebrites* Marshall, 1926, type species *V. murdocki* Marshall, having been included in that genus at its establishment. *V. murdocki* is characterized by a serpenticone shell form with strongly depressed volutions persisting throughout all known ontogenetic stages to a shell diameter of 4·5 cm (Henderson 1970). It has conspicuous lirae on the flanks which split into very fine subdivisions at the margin of the venter. Arkell, Kummel and Wright (1957, fig. 230.3*d*) and Henderson (1970, text-fig. 5*c*) misrepresented the internal suture of *V. murdocki*, marking the umbilical seam as the internal lobe. Its suture (Marshall 1926, pl. 19, fig. 9; redrawn by Wiedmann 1962*b*, text-fig. 4*i*) is like that of *G. varicostatum* (Kennedy and Klinger 1979, text-fig. 1) and *Anagaudryceras particostatum* (Henderson 1970, text-fig. 5*b*).

The type series of *G. kayei*, now held by the British Museum (Natural History), contains only juvenile specimens, the largest of which is 55 mm in diameter. Larger specimens from Western Australia show that the juvenile serpenticone, with depressed volutions, strongly convex flanks, and a broadly arched venter, changes at a shell diameter of about 70 mm to a less widely umbilicate adult growth stage with equidimensional whorls showing gently convex flanks and a more narrowly arched venter. *G. kayei* is comparable with *G. varicostatum* van Hoepen (redescribed by Kennedy and Klinger 1979) except that the serpenticone shell form and fine ornament persist to a later stage of ontogeny. Separate generic status for *kayei* is not warranted for such minor differences and it is regarded here as a member of *Gaudryceras*.

V. murdocki probably represents a *Gaudryceras* in which the paedomorphic tendencies of *G. kayei* are even more advanced. Larger specimens than currently available are needed to confirm its status and *Vertebrites* is perhaps best treated provisionally as a monotypic subgenus of *Gaudryceras*.

Gaudryceras sp.

Material. One specimen, WAM 83.3144, from locality 16.

Description. The specimen represents the last quarter whorl of a phragmocone which would have measured some 17 cm in diameter with an umbilical diameter of approximately 6 cm. Whorl profile compressed, with a whorl breadth/whorl height ratio of 0·75. Umbilical wall low and outwardly sloping, umbilical shoulder rounded, flanks weakly convex and slightly convergent, and venter well-rounded. Fine, dense ribs, some eighty per half whorl, begin from the umbilical seam. They are weakly prorsiradiate on the umbilical wall, shoulder, and dorsal flanks, straighten at the mid-flank, and swing slightly forward on the ventral flanks to be weakly projected across the venter. There is a single constriction with the same course as the ribs, preceded by a collar. Suture is deeply cut and highly dissected with L bifid.

Remarks. The specimen is a member of the *G. mite* species group of Kennedy and Klinger (1979) but more material is needed before its specific identity can be satisfactorily established. It may be compared with *G. beantalyense* Collignon (1956) but appears to differ in having less flexuous ribbing and lacking intercalatory ribs which appear on the dorsal flanks of the Madgascan species. It also resembles *G. vararaqurense* Kossmat (1895) but is less finely ribbed.

Family TETRAGONITIDAE Hyatt, 1900
Genus PSEUDOPHYLLITES Kossmat, 1895

Type species. *Ammonites indra* Forbes, 1846.

Remarks. Many of the species proposed for *Pseudophyllites* have passed into synonymy (Henderson 1970; Kennedy and Klinger 1977*b*) so that at present only three are regarded as valid. *P. indra* (Forbes) was widely distributed on the margins of north Pacific and Indian Oceans and ranged into Europe as far north as Poland and possibly as far west as south-eastern France. *P. latus* (Marshall) had a southern distribution (Antarctic Peninsula, southern Argentina, New Zealand, south-eastern Africa, Madagascar, and Western Australia) and was also represented in Greenland. Its disjunct distribution is reminiscent of the bipolar species distribution shown by planktonic Foraminifera (Bé 1977) and other microplankton. *P. teres* (van Hoepen) is known with certainty only from south-eastern Africa and Madagascar. *P. amphitrite* and *P. nereidideditus*, established by Maury (1930) for two Brazilian specimens, are of uncertain affinities. They may represent a separate local species or they may be junior synonyms as suggested by Kennedy and Klinger (1977*b*); more material is needed to assess their status. The Austrian species *P. pastremus* (Redtenbacher 1873) is known only from poorly preserved material and is also a *nomen dubium*.

Pseudophyllites latus (Marshall, 1926)

Plate 3, figs. 1–3, 6–8; text-fig. 5b, c

1926 *Tetragonites latus* Marshall, p. 149, pl. 20, fig. 6, 6*a*; pl. 32, figs. 1, 2.
1965 *Pseudophyllites peregrinus* Spath; Hünicken, p. 53, pl. 1, figs. 5–7; pl. 7, figs. 3, 4.
1970 *Pseudophyllites latus* (Marshall); Henderson, p. 12, pl. 1, fig. 10*a*, *b*; pl. 2, fig. 3; text-fig. 4*a*, *c*.
1977*b* *Pseudophyllites latus* (Marshall); Kennedy and Klinger, p. 190, text-figs. 25, 26.

Material. Eight specimens, localities 6, 12, 16, 17, 19, and 23.

Description. Whorls equidimensional to slightly depressed, with a broadly arched venter. Umbilical wall vertical at the seam but curving outwards to merge with a broadly rounded umbilical shoulder. Umbilicus measures more than 20 % of the shell diameter in early ontogeny, reducing to 19 % at a shell diameter of 70 mm. Ornament is lacking. Septal recess and inner septum small for the genus; width of the latter is about 24 % of the whorl diameter. External saddle of the suture is broad and spatulate; E is broad, L bifid, and U has its auxiliary elements arrayed in a rectilinear series.

Dimensions.

	D	H	B	B/H	U	%
WAM 81.2514	28·0	12·5	15·0	1·25	6·2	22
WAM 83.2692	40·0	20·5	20·5	1·00	7·8	20
WAM 83.2693	56·2	28·5	28·5	1·00	10·5	19
NMV P31019	70·0	35·0	36·0	1·02	13·0	19

Remarks. Morphological differences between *P. latus* and *P. indra* are subtle, involving slight chances in whorl proportions and shape, the size of the septal recess and inner septum, and the shape of the ventral saddle. This notwithstanding, morphology within each of the species is so consistent, even in disparate populations, that they are readily separable.

The range of *P. latus* is upper Santonian–lower Maastrichtian.

Pseudophyllites indra (Forbes, 1846)

Plate 2, figs. 7, 8;, Plate 3, figs. 4, 5; text-fig. 5*a*, *d*

1846 *Ammonites indra* Forbes, p. 105, pl. 11, fig. 7*a–c*.
1977*b* *Pseudophyllites indra* (Forbes); Kennedy and Klinger, p. 182, text-figs. 19*a–f*, 20–22.
1980 *Pseudophyllites indra* (Forbes); Blaszkiewicz, p. 19, pl. 44, fig. 1.

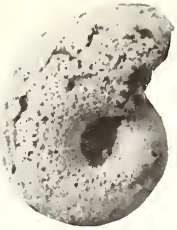
Material. Seventy-two specimens, localities 3–7, 9–18, 20–23, and 25.

Description. Whorls very slightly compressed with a narrowly arched venter; umbilical wall curving gently outwards to a broadly rounded umbilical shoulder. Initial growth stages have an umbilicus measuring some 22 % of the shell diameter, reducing to 16 % at a shell diameter of 118 mm. Septal recess and inner septum large; width of the latter measures some 36 % of the whorl width. Suture with a narrow lanceolate external saddle; E is narrow, L bifid, and U is slightly retracted on the umbilical wall.

EXPLANATION OF PLATE 3

Figs. 1–3, 6–8. *Pseudophyllites latus* (Marshall). 1–3, WAM 81.2514, × 1. 6–8, NMV P31019, × 1.
Figs. 4–5. *P. indra* (Forbes), WAM 60.44a, × 1.

PLATE 3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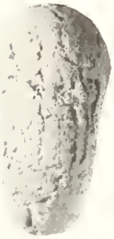
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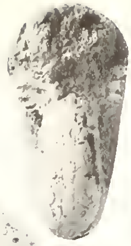
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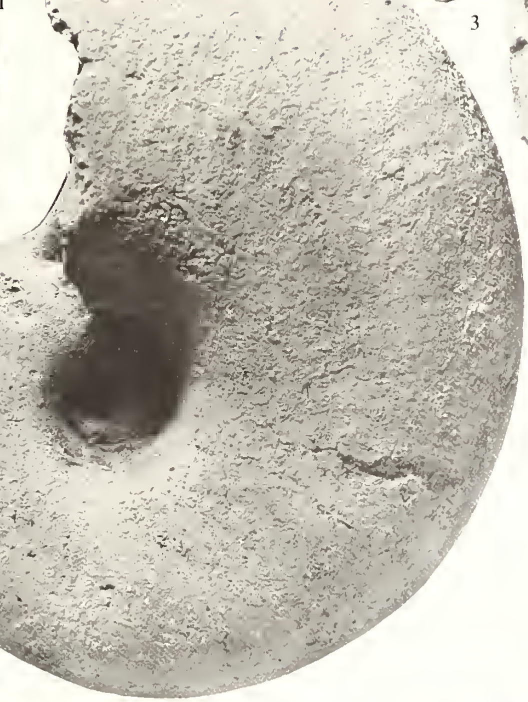
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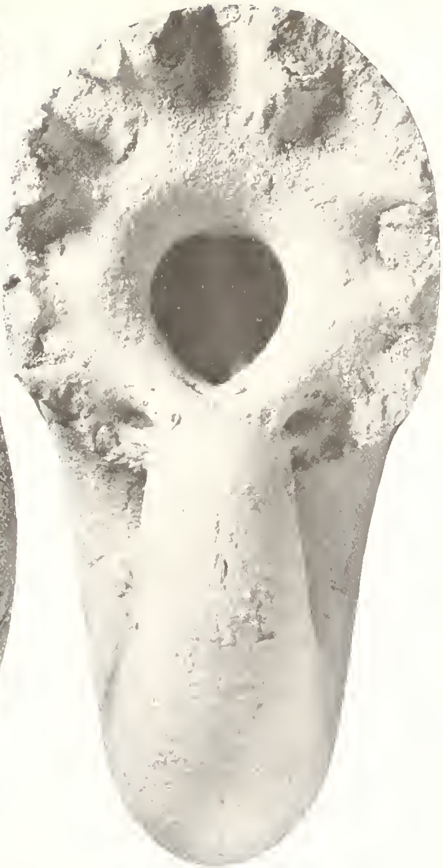
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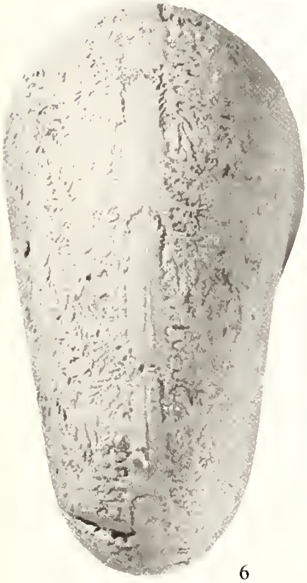
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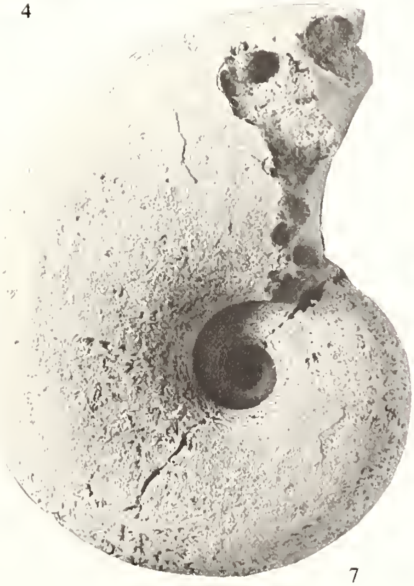
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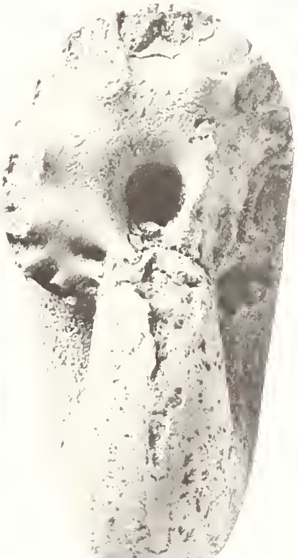
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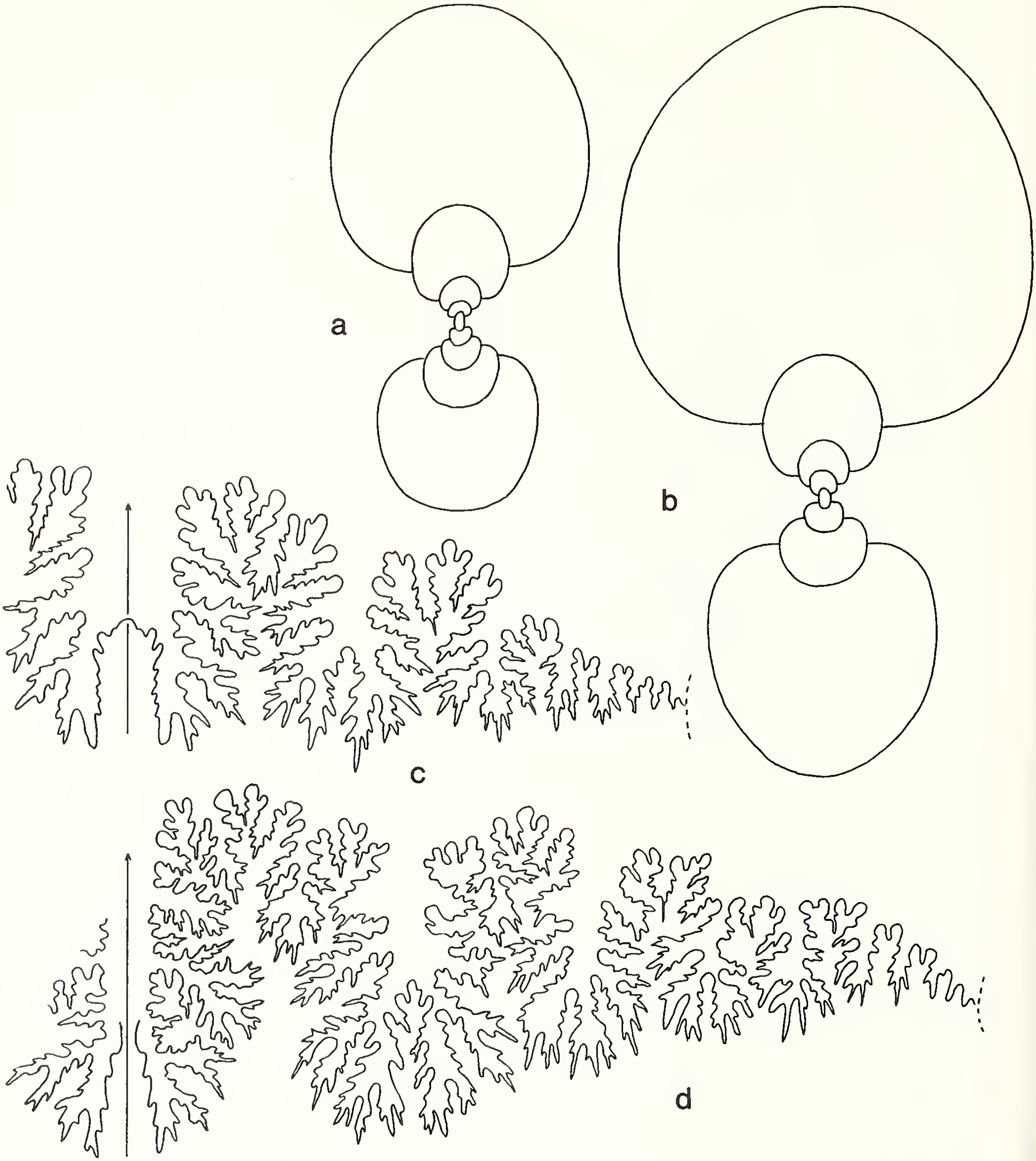
HENDERSON and McNAMARA, *Pseudophyllites*



TEXT-FIG. 5. Whorl profiles and sutures of *Pseudophyllites*. *a*, *P. indra* (Forbes), WAM 81.2433, ×1·5. *b*, *P. latus* (Marshall), NMV P31019, ×1·5. *c*, *P. latus* (Marshall), NMV P31019, ×3. *d*, *P. indra* (Forbes), WAM 81.2433, ×3.

Dimensions.

	D	H	B	B/H	U	%
WAM 81.2497	30·8	15·2	14·8	0·97	7·0	23
WAM 81.2358	43·0	21·5	20·8	0·97	9·0	21
WAM 60.92d	52·0	27·5	27·0	0·98	10·5	20
WAM 10571	70·0	35·8	33·5	0·94	13·0	19
WAM 80.972	80·5	41·5	39·0	0·94	15·2	19
WAM 81.2609a	91·0	47·5	46·2	0·97	16·8	18
Lectotype: BM C51068	110·0	58·0	54·0	0·93	18·0	16
WAM 60.44a	110·0	58·5	56·0	0·96	20·0	18
WAM 60.44b	116·0	66·0	58·0	0·97	22·0	19
WAM 81.2500	172·0	98·0	96·0	0·98	27·5	16

Remarks. The Western Australian suite matches exactly with Forbes's original type series comprised of more than twenty-five specimens and held by the British Museum (Natural History). It displays the complex lytoceratid septal surface in exceptional detail, as described elsewhere (Henderson 1984).

Specimens retaining the shell show that weak ribs appear on the flanks at a shell diameter of about 40 mm. The largest specimen is still separate at a shell diameter of 17·2 cm, indicating that adult members of the species must have reached diameters of 25 cm or more.

P. indra has an established range of early Campanian–Maastrichtian. In south-eastern Africa its range may perhaps extend down into the later Santonian (Kennedy and Klinger 1977*b*).

Suborder AMMONITINA Hyatt, 1889
Superfamily DESMOCERATACEAE Zittel, 1895
Family DESMOCERATIDAE Zittel, 1895
Subfamily DESMOCERATINAE Zittel, 1895
Genus DESMOPHYLLITES Spath, 1929

1894 *Schluteria* de Grossouvre (*non* Fritsch 1887), p. 216.
1938 *Schlutericeras* Collignon (*non* Hyatt 1903), p. 92.

Type species: *Desmoceras larteti* Seunes, 1891.

Remarks. *Desmophyllites* is little different from *Desmoceras* (*Pseudouhligella*) Matsumoto, 1942*a*, being distinguished only by its more embracing volutions and narrower umbilicus, the wall of which has its upper portion sloping outwards and passing into the umbilical shoulder in a smooth curve. In *Desmoceras* (*Pseudouhligella*) the umbilical wall is vertical and the shoulder abrupt. The internal suture of *Desmoceras* (*Pseudouhligella*) has not as yet been described but it probably has fewer auxiliary divisions of the umbilical lobe than that of *Desmophyllites*.

As noted by Matsumoto (1954*a*), the ranges of these two taxa are disjunct, *Desmophyllites* ranging no lower than Santonian and *Desmoceras* (*Pseudouhligella*) ranging no higher than Cenomanian. It may be that *Damesites* Matsumoto, 1942*a* was the progenitor of *Desmophyllites*. It is well known from Turonian and Coniacian strata and differs from *Desmophyllites* only in possessing a keel. Body chambers of *D. diphylloides* with a weak mid-ventral ridge described by Matsumoto (1959*b*) from California offer some support to this proposal.

Only two named species of *Desmophyllites* are recognized here: *D. larteti* (Seunes) characterized by compressed whorls with a B/H ratio of 0·5–0·6 at a shell diameter of some 8 cm and *D. diphylloides* (Forbes) which is less compressed, its whorls having a B/H ratio of 0·7–0·8 at a comparable shell size. Only two specimens of *D. larteti*, both from Maastrichtian chalk facies in France, have been described. It is possible that they represent *D. diphylloides* flattened by compression and they need re-evaluation. The fragmentary specimen described from the Antarctic Peninsula by Howarth (1958) is more widely umbilicate than either *D. diphylloides* or *D. larteti* and appears to represent an undescribed species.

Desmophyllites diphylloides (Forbes, 1846)

Plate 4, figs. 1–4

1846 *Ammonites diphylloides* Forbes, p. 105, pl. 8, fig. 8*a–c*.
1894 *Desmoceras pyrenaicum* de Grossouvre (*pars*), p. 168, pl. 37, fig. 9*a–c* (*non* pl. 25, fig. 2*a*, *b*).
1898 *Desmoceras phyllimorphum* Kossmat, p. 110, pl. 19, fig. 10*a–c*.
1921 *Schluteria woodsi* Spath, p. 45, fig. 1.
1938 *Schluteria larteti* (Seunes); Collignon, p. 42, pl. 7, fig. 3, 3*a*, text-figs. K, L.
1959*b* *Desmophyllites diphylloides* (Forbes); Matsumoto, p. 9, pl. 3, fig. 3*a–c*, text-fig. 2.
1931 *Desmophyllites diphylloides* var. *besairiei* Collignon, p. 15, pl. 2, fig. 8, 8*a*, *b*; pl. 8, figs. 5–8.
1961 *Desmophyllites diphylloides* var. *inermis* Collignon, p. 63, pl. 24, figs. 4, 4*a*, 4*b*, 5, 5*a*, 5*b*; pl. 25, fig. 3, 3*a*, 3*b*.
1961 *Desmophyllites diphylloides* var. *lata* Collignon, p. 64, pl. 25, figs. 7, 7*a*, 7*b*, 8, 8*a*, 8*b*, text-fig. 4.
1961 *Desmophyllites phyllimorphus* (Kossmat); Collignon, p. 65, pl. 26, fig. 1, 1*a*, *b*, text-fig. 5.
1961 *Desmophyllites larteti* (Seunes); Collignon, p. 66, pl. 26, fig. 2, 2*a*, *b*, text-fig. 6.
1963 *Desmophyllites phyllimorphus* (Kossmat); Jones, p. 34, pl. 10, figs. 4–6.
1965 *Desmophyllites diphylloides* (Forbes); Howarth, p. 388, pl. 11, fig. 3*a*, *b*.
1980 *Desmophyllites diphylloides* (Forbes); Blasco *et al.*, p. 483, pl. 2, figs. 9–15.

Material. Thirty-two specimens, localities 4–9, 11, 12, 15–18, 20, 23, and 25.

Description. Umbilicus a steep-walled pit measuring 7–9 % of the shell diameter. Whorls embracing with very weakly convex, subparallel flanks and a broadly arched venter; they are compressed with the whorl breadth/whorl height ratio reducing from about 0·87 at a shell diameter of 20–25 mm to about 0·76 at a shell diameter of 75 mm. Axis of maximum whorl width is slightly ventral of the mid-flanks. Shell smooth apart from shallowly impressed constrictions which are weakly flexuous on the flanks and quite strongly projected on the venter. Suture with finely divided elements. E almost as deep as L which is trifid, U has some fifteen auxiliary saddles, and I is bifid.

Dimensions.

	D	B	H	B/H	U	%
Lectotype: BM C22682	20·2	10·8	9·2	0·85	1·2	5
WAM 80.837	24·5	12·5	10·8	0·86	1·5	6
WAM 81.2618	35·0	18·0	15·5	0·86	2·0	6
WAM 71.212	40·5	20·5	17·2	0·86	3·2	8
WAM 81.2680	46·0	24·5	19·2	0·78	4·0	9
WAM 60.92a	51·0	26·0	21·5	0·83	4·5	9
WAM 81.2520	61·0	32·0	26·2	0·82	5·2	8
WAM 81.2694	70·0	37·0	29·2	0·77	5·8	8
WAM 60.52a	75·0	40·0	32·8	0·82	6·0	8
WAM 81.2600	77·0	41·0	31·2	0·76	6·0	8

Remarks. Forbes's type series from Pondicherry, India, now held by the British Museum (Natural History), are all juvenile specimens and the lack of adults has in the past resulted in uncertainty in the definition of the species. The Western Australian suite allows documentation of the shell ontogeny to a diameter of nearly 8 cm. Whorls become more slender with growth. They all show weakly convex flanks but among the specimens, especially juveniles, the convexity is slightly variable. The number and shape of constrictions is also variable. They show clearly only on internal moulds and are more

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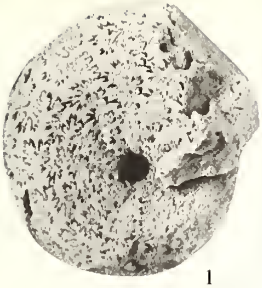
EXPLANATION OF PLATE 4

Figs. 1–4. *Desmophyllites diphylloides* (Forbes). 1–2, WAM 81.2449, × 1. 3–4, WAM 81.2694, × 1.

Figs. 5–6, 9–10, 14–15. *Kitchinites spathi* sp. nov. 5–6, paratype, WAM 71.209a, × 1. 9–10, holotype, WAM 84.632, × 1. 14–15, paratype, WAM 71.209b, × 1.

Figs. 7–8, 11–13. *Maorites densicostatus* (Kilian and Reboul). 7–8, WAM 80.847, × 1. 11–13, WAM 80.1000, × 1.

PLATE 4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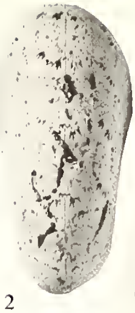
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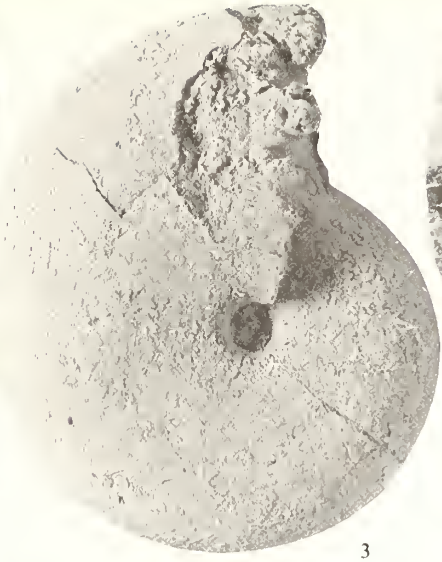
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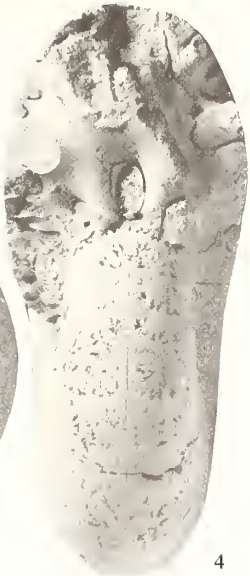
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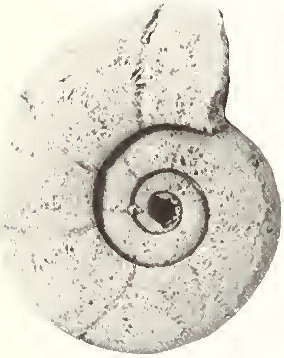
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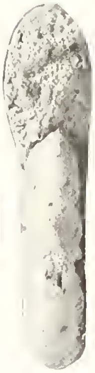
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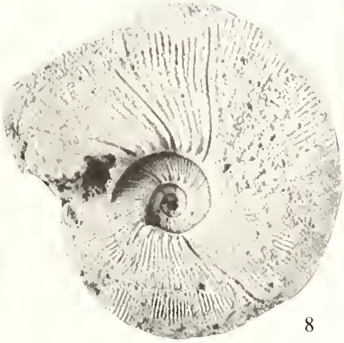
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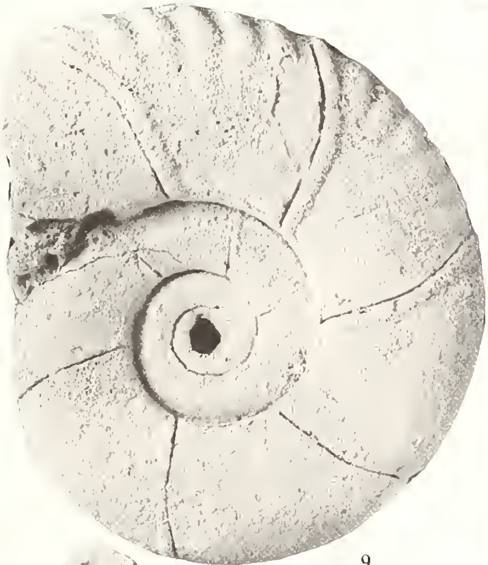
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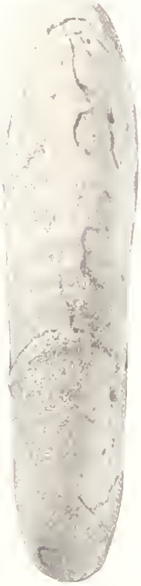
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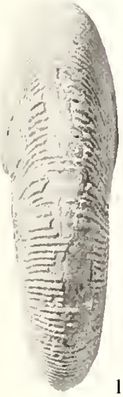
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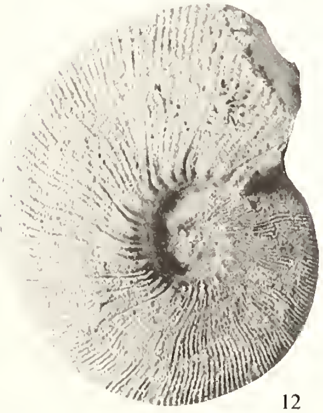
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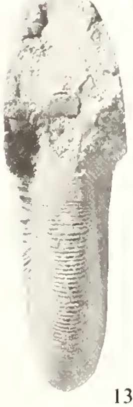
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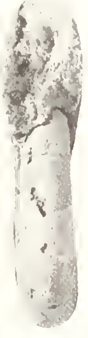
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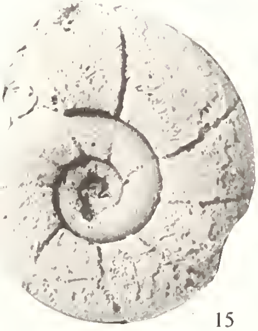
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HENDERSON and McNAMARA, Desmoceratidae and Kossmaticeratidae typical of juveniles which have as many as eight per whorl rather than adult whorls which may show as few as two. On some shells they are quite flexuous on the flanks whereas on others they are almost straight. The umbilical wall is convex, overhanging near the umbilical seam, and turned outwards near the umbilical shoulder. Measurements of the umbilicus given here represent minimum diameters; measurements in the literature suggesting a wider umbilicus for *D. diphylloides* were doubtless taken at the base of the umbilical shoulder.

The ontogenetic change in whorl shape and variation in constrictions shown by the Western Australian specimens necessitate a wider definition of *D. diphylloides* than that adopted by most previous commentators. The large, slender whorled specimen from Trichonopoly, India, on which Kossmat (1898) based *D. phyllimorphum*, is best regarded as an adult *D. diphylloides*. It has a whorl breadth/whorl height ratio of 0·70 at a shell diameter 81·5 mm and is only slightly more compressed than Western Australian specimens of equivalent size. The large Alaskan specimens recorded by Jones (1963) as *D. phyllimorphum* because of their slender whorls are likewise adult *D. diphylloides*. Juvenile *Desmophyllites* from the Pacific coast of North America, originally described by Whiteaves (1879), Usher (1952), and Anderson (1958) as local species, were united with *D. diphylloides* by Matsumoto (1959*b*).

Slight changes in whorl shape and the nature of constrictions, used by Collignon (1931, 1938, 1961, 1966, 1971) to descriminate no less than three species and four varieties of *Desmophyllites* from Madagascar, are treated here as representing intraspecific variation within a single species of which *D. diphylloides* is the senior synonym. New species erected by van Hoepen (1921) and Spath (1921) from south-eastern Africa are also regarded as falling within the compass of *D. diphylloides* (see Matsumoto 1959*b*), as is the specimen figured by de Grossouvre (1894, pl. 37, fig. 9*a–c*) as *Desmoceras pyrenaicum* but unrelated to the primary type of that species (de Grossouvre 1894, pl. 25, fig. 2*a*, *b*).

Desmophyllites diphylloides was widely distributed on the margins of the Indian and Pacific Oceans and spread westward along the Tethyan seaway to reach North Africa and southern France. It has an established range of lower Santonian–Maastrichtian.

Subfamily PUZOSIINAE Spath, 1922

Genus KITCHINITES Spath, 1922

1922 *Kitchinites* Spath, p. 127.
1954*b* *Neopuzosia* Matsumoto, p. 89.
?1953 *Oiophyllites* Spath, p. 21.

Type species. Holcodiscus pondicherryanus Kossmat, 1897a.

Remarks. Neopuzosia, with type species *N. japonicus* (Spath), was introduced by Matsumoto (1954*b*) to separate Japanese Santonian–lower Campanian species from Campanian–Maastrichtian *Kitchinites* (*s.s.*). Howarth (1965), however, convincingly argued that these two taxa are better treated as synonyms, rather than as subgenera of *Kitchinites* (*s.l.*) as has been common practice.

Oiophyllites Spath (1953) was based on *O. decipiens* Spath known only from juvenile specimens from the Antarctic Peninsula, the largest of which measures 20 mm in diameter. A second species, *O. angolaensis* Spath (1953), was based on a single juvenile specimen from Angola, 21 mm in diameter. *Oiophyllites* differs from *Kitchinites* principally in having a smooth shell. However, in some species of *Kitchinites*, such as *K. darwini* (Steinmann) (redescribed by Howarth 1966), the juvenile shell is smooth to a diameter of 30 mm. It therefore seems likely that both *Oiophyllites* species are merely juvenile *Kitchinites*. It is noteworthy that *Oiophyllites* and large *Kitchinites* are known from the same locality in Angola (Howarth 1965) and occur at separate but broadly coeval localities in the Antarctic Peninsula (Howarth 1966).

Kitchinites is little different from its presumed ancestor *Mesopusozia* Matsumoto (1954*b*), based on the Turonian–Coniacian species *M. pacifica* Matsumoto. The whorl profile of *Mesopusozia*, which is rounded rather than compressed, allows its separation.

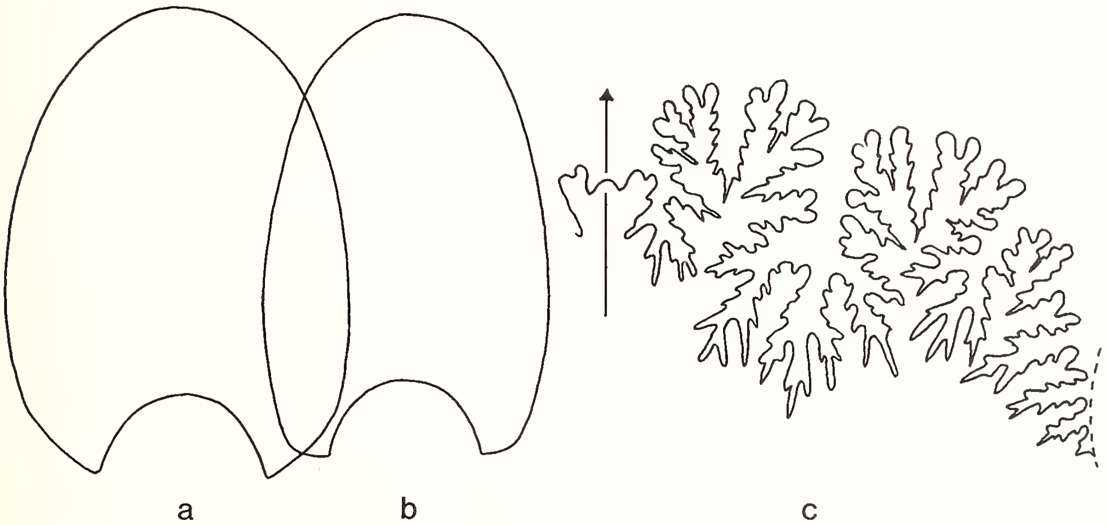
Sixteen nominate species of *Kitchinites* (= *Neopusozia*) have been proposed in all if the Western Australian species described here is included. Six were described from Madagascar by Collignon (1961) but all are round-whorled taxa and better transferred to *Mesopuzosia*. The remainder are distributed on the borderlands of the Indo-West Pacific and South Atlantic Oceans, having been recorded from Saghalien, Hokkaido, New Zealand, Western Australia, India, Angola, the Antarctic Peninsula, and southern South America. They range in age from Santonian to Maastrichtian.

Kitchinites spathi sp. nov.

Plate 4, figs. 5, 6, 9, 10, 14, 15; text-fig. 6*b*, *c*

1941 *Hauericeras* sp. Spath, p. 43.
1941 *Kitchinites* sp. Spath, p. 45.

Material. Holotype WAM 84.632, locality 8. Paratypes WAM 81.2410, locality 4; WAM 81.2703, locality 6; WAM 71.209a, 71.209b, locality 8; NMV P31022, locality 11; WAM 80.971, 80.995, locality 12; WAM 81.2630, locality 15; WAM 10572, locality 16. Thirty-five additional specimens, localities 3–5, 7, 9, 10, 12, 16–18, 20, and 23–25.



TEXT-FIG. 6. *a*, whorl profile of *Neograhamites carnarvonensis* sp. nov., holotype, WAM 80.840, ×4. *b*, whorl profile of *Kitchinites spathi* sp. nov., paratype, WAM 80.971, ×2. *c*, suture of *K. spathi* sp. nov., paratype, WAM 71.209a, ×4.

Description. Shell evolute and discoidal with whorl breadth/whorl height 0·63–0·76 and the umbilicus measuring 37–42% of the shell diameter. Umbilical wall low, subvertical, and sharply reflected at the umbilical shoulder which is narrowly rounded. Flanks subparallel and very weakly convex; venter smoothly rounded. Early whorls have no ribs apart from growth lines, but broad, rounded costae, numbering about twenty per half whorl and confined to the ventral flanks and venter, appear at a shell diameter of 60 mm. Initially costae are prorsiradiate but they bend forward at the margin of the venter across which they are gently projected. Narrow constrictions, each preceded by a prominent collar, number three to six per half whorl beginning at a shell diameter of less than 1 cm. They are prorsiradiate and almost straight across the umbilical wall and flanks and are strongly projected across the venter where they commonly truncate one rib. Suture with finely divided minor elements for the genus and a strongly retracted suspensive lobe.

Dimensions.

	D	H	B	B/H	U	%
WAM 81.2703	27·0	9·5	7·0	0·73	10·8	40
WAM 81.2630	36·5	11·8	9·0	0·76	14·8	41
NMV P31022	40·0	14·5	10·5	0·72	15·0	37
WAM 80.995	42·0	15·5	10·0	0·64	15·8	38
WAM 71.209a	47·0	11·0	15·5	0·71	19·0	40
NMV P31015	52·0	17·0	11·0	0·65	22·0	42
NMV P31013	76·0	26·0	17·8	0·68	30·5	40
WAM 10572	84·5	29·8	19·2	0·64	33·5	40

Remarks. Whorl dimensions are somewhat variable between different specimens but whorl breadth/whorl height ratio tends to reduce as ontogeny proceeds. The most mature whorl fragment in the collection shows that the strong costation persists to a shell diameter of some 105 mm at least.

The suite of specimens now available shows that the juvenile and adult whorl fragments described by Spath (1941) as *Hauericeras* sp. and *Kitchinites* sp. respectively are conspecific.

K. spathi is related to *K. darwini* (Steinmann) (redescribed by Howarth 1966), *K. angusta* (Marshall) (redescribed by Henderson 1970), and *K. angolaensis* Howarth 1965, in which the ribs are restricted to the ventral flanks and venter for at least part of the ontogeny. In *darwini* and *angolaensis* the ribs are more subdued and more closely spaced than in *spathi*. *K. augusta* is distinguished from *spathi* in being more narrowly umbilicate and having thinner costae which are more strongly projected across the venter.

Family KOSSMATICERATIDAE Spath, 1922
Subfamily KOSSMATICERATINAE Spath, 1922
Genus GUNNARITES Kilian and Reboul, 1909

1909 *Gunnarites* Kilian and Reboul, p. 26.

Type species. G. antarcticus (Weller, 1903, p. 417, pl. 11, figs. 1, 2).

Remarks. Western Australian *Gunnarites* are allied to taxa from the Antarctic Peninsula. Species determination, however, has been poorly documented for the Antarctic suite and subject to widely differing views. Kilian and Reboul (1909), in establishing the genus, recognized *G. antarcticus* (Weller) and *G. kalika* (Stoliczka) as well as three varieties to express variation in *G. antarcticus*. A third species, *G. gunnari*, they mistakenly referred to *Kossmaticeras*. Spath (1953) raised one of Kilian and Reboul's *antarcticus* varieties, var. *bhavaniformis*, to species rank and introduced four new species to make a total of eight. In addition, Spath introduced a plethora of varieties to cover specimens of intermediate morphology.

Howarth (1966) rationalized the suite to five species, three of which display appreciable intraspecific variation: *G. kalika* Stoliczka (= *Maorites pseudobhavani* Spath), *G. antarcticus* Weller (= *G. paucinodatus* Spath, *G. rotundus* Spath, and *G. flexuosus* var. *transitoria* Spath), *G. bhavaniformis* Kilian and Reboul (= *G. flexuosus* Spath), *G. gunnari* (Kilian and Reboul), and *G. pachys* Spath.

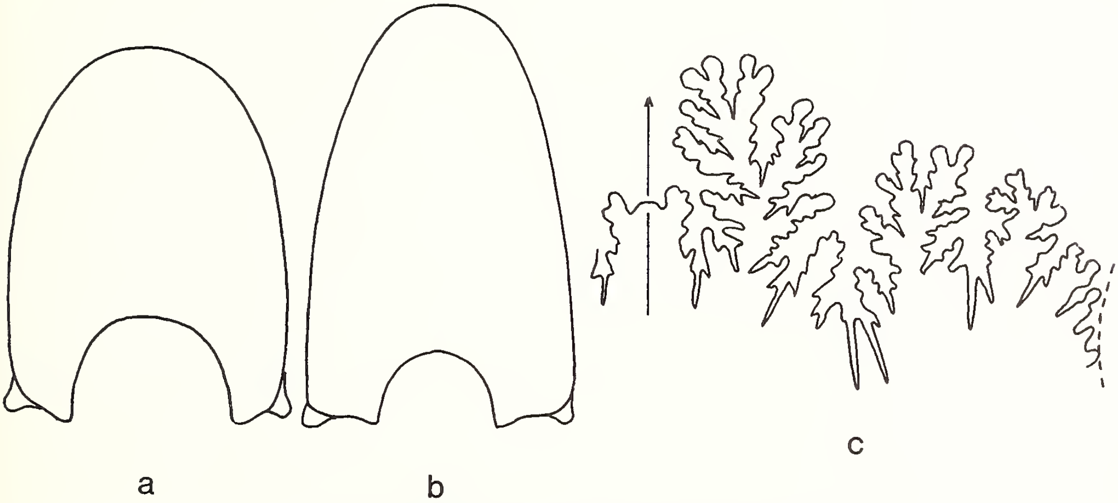
One of us (R.A.H.) has re-examined the Antarctic Peninsula collections on which Spath worked, held by the British Museum (Natural History), and generally endorses Howarth's (1966) synonymies. Shell measurements and rib counts, however, show that the range of variation between Antarctic specimens referred to *kalik* and *bhavaniformis* is continuous (text-fig. 8). They are treated here as a single variable species under the name *bhavaniformis*, and considered distinct from *G. kalika* Stoliczka. The status of *G. rotundus* is questionable. The type series consists of internal moulds but one specimen, BM C41370, retains fragments of shell showing that the ribs are not crenulate on the venter up to a shell diameter of 35 mm. This species is more likely to represent *Kossmaticeras* (*Natalites*) than *Gunnarites*.

Gunnarites kalika (Stoliczka, 1865)

Plate 5, figs. 8–15; text-figs. 7*b*, *c*, 8

	1865	*Ammonites kalika* Stoliczka, p. 140, pl. 70, fig. 5*a*, *b*.
non	1909	*Gunnarites kalika* Stoliczka; Kilian and Reboul, p. 34.
	1936	*Gunnarites* [*sic*] *kalika* Stoliczka; Whitehouse *in* Raggatt, p. 160.
	1941	*Kossmaticeras* sp. nov.? aff. *aemilianus* Stoliczka; Spath, p. 44, pl. 1, fig. 2*a*, *b*.
non	1953	*Gunnarites kalika* Stoliczka; Spath, p. 33, pl. 10, figs. 1–6.
non	1966	*Gunnarites kalika* Stoliczka; Howarth, p. 67.
	1980	*Gunnarites* sp. cf. *kalika* Stoliczka; Klinger *et al.*, p. 299, text-figs. 6A, B.
non	1980	*Gunnarites kalika* Stoliczka; Blasco *et al.*, p. 487, pl. 4, figs. 2–4.

Material. One hundred and sixty-one specimens, localities, 1, 3–20, and 22–25.



TEXT-FIG. 7. *a*, whorl profile of *Gunnarites bhavaniformis* (Kilian and Reboul), BM C41333, ×2. *b*, whorl profile of *G. kalika* (Stoliczka), NMV P31026, ×2. *c*, Suture of *G. kalika* (Stoliczka), WAM 81.2404, ×4.

Description. Shell discoidal with whorl breadth/whorl height ratio of 0·6–0·76, and involute with the umbilical diameter 21–26% of the shell diameter. Umbilical wall vertical, or overhanging where it is produced into umbilical bullae; flanks weakly convex, converging towards the venter which is narrowly rounded. Twenty to twenty-five bullae per whorl mark the umbilical shoulder, each typically with a slight rursiradiate inclination. Segments of the umbilical shoulder are straight on many specimens giving the umbilicus a polygonal appearance. Ribs are slender and closely spaced, prorsiradiate and slightly flexuous. They number forty-one to seventy-two per half whorl, springing in bundles of three to five from the umbilical bullae with occasional intercalatories appearing in the mid-flank region. On the flanks they display smooth crests but are finely crenulate across the venter. Six to eleven somewhat flexuous constrictions per whorl, narrow on surfaces retaining shell and broader on internal moulds. Each is bordered by ridges, that on the adapical side typically being the strongest. Constrictions are more strongly prorsiradiate than the ribs so that three to five of the latter are truncated. Suture florid and deeply incised with lobe terminations overprinting the saddle extremities of the previous suture; E is broad and shallower than L and it is strongly retracted on the umbilical wall.

Dimensions. See text-fig. 8.

Remarks. The abundant material allows documentation of intraspecific variation. Shell shape is relatively constant across the suite but the density of ribbing shows very wide variation between individual specimens (text-fig. 8). The largest specimen (WAM 81.2636; pl. 5, fig. 15) has part of the body chamber preserved and perhaps shows a mature ornament. Some of the ribs on the last segment of preserved whorl become feeble. The number of ribs on the last half-whorl (forty-one) and the number of constrictions (seven) represent the extreme limit of variation whereas the inner whorls are more densely ribbed and carry few constrictions. The south-eastern African specimen of *G. kalika* described by Kennedy and Klinger (in press) likewise has sparse ribbing on the last half whorl compared with earlier volutions and the last segment of preserved whorl is marked by feeble ribbing. Crenulation of the ribs has not been confirmed for shell diameters less than 3 cm and juvenile shells might easily be confused with *Maorites*.

The identity of these West Australian specimens with *G. kalika*, which was described from a single south Indian specimen, is clear from their shell dimensions and ornament (text-fig. 8). Spath (1941) mistakenly referred the species to *Kossmaticeras*, doubtless because the specimens at his disposal were internal moulds and did not show the distinctive rib crenulation.

The Antarctic Peninsula *G. kalika* of Kilian and Reboul (1909) and Spath (1953) (= *M. pseudobhavani* Spath, see Howarth 1966, p. 67) are here considered to be conspecific with *G. bhavaniformis* Kilian and Reboul. The range of variation in shell characteristics is continuous between specimens referred to these two species by Spath and consistently different from the population of Western Australia *G. kalika* to which Stoliczka's type specimen clearly belongs (text-fig. 8). The name *bhavaniformis* is retained for the Antarctic species. The Patagonian specimen referred to *G. kalika* by Blasco *et al.* (1980) develops very coarse ribbing at a shell diameter less than 50 mm after a finely ribbed initial stage of growth. It appears to be unrelated to either *G. bhavaniformis* Kilian and Reboul, or *G. kalika*, as redefined here.

G. kalika is known from the early Maastrichtian of south-eastern Africa (Klinger *et al.*, 1980; Kennedy and Klinger in press) and of Western Australia. The Indian type specimen is from the Ariyalur stage and is probably also of Maastrichtian age.

Gunnarites raggatti sp. nov.

Plate 6, figs. 1–4, 9, 10

?1980 *Gunnarites kalika* Stoliczka; Blasco *et al.*, p. 487, pl. 4, figs. 2–4.

Material. Holotype WAM 81.2542, locality 5. Paratypes UWA 97367, locality 1; WAM 81.2513, locality 5; WAM 81.2645, locality 6; WAM 83.2708, locality 25.

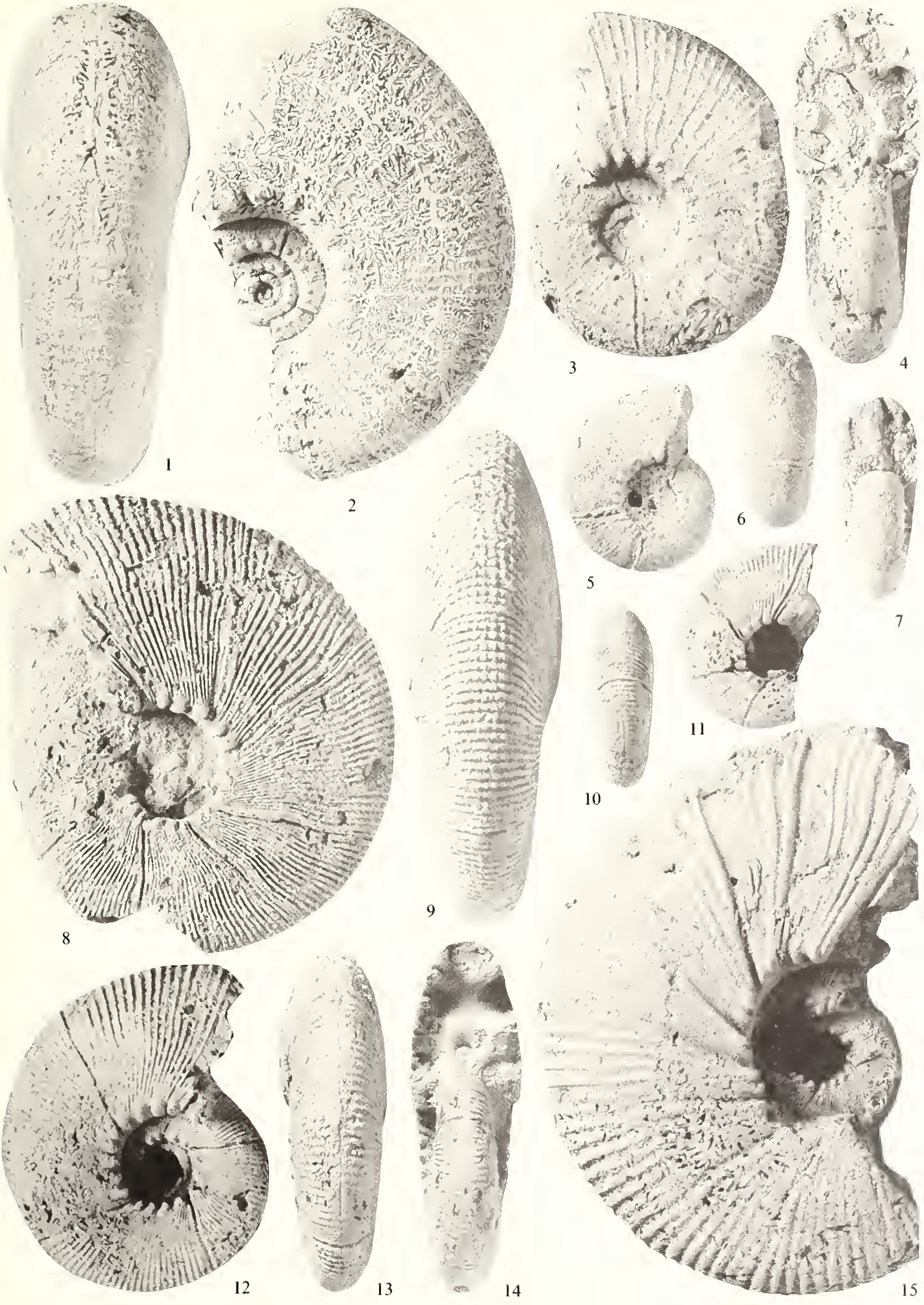
Description. Juvenile growth stages, up to a shell diameter of 40 mm, have an almost equidimensional whorl profile and are evolute with the umbilical diameter measuring 36% of the shell diameter. During later growth, the whorl section becomes compressed and the coiling slightly more involute, the umbilical diameter reducing to 33% of the shell diameter. Umbilical wall subvertical, umbilical shoulder abrupt, flanks flattened and slightly convergent, and venter broadly rounded. Ribs are thin and sharp, separated by broad interspaces and finely crenulate on the venter and ventral flanks. They swing gently forward from the umbilical shoulder and straighten in the mid-flank region to be rectiradiate across the venter. On juvenile whorls, up to a shell diameter of 40 mm, they number seventy-five to eighty per whorl, springing in bundles of three and four from ten to eleven umbilical bullae with as many as five additional ribs arising from the umbilical shoulder between bullae.

EXPLANATION OF PLATE 5

Figs. 1–7. *Grossouvrites gemmatus* (Huppé). 1–2, WAM 80.842, ×1. 2–3, WAM 81.2521, ×1. 5–7, WAM 81.2634, ×1.

Figs. 8–15. *Gunnarites kalika* (Stoliczka). 8–9, NMV P31012, ×1. 10–11, WAM 81.2496, ×1. 12–14, NMV P31026, ×1. 15, WAM 81.2636, ×1.

PLATE 5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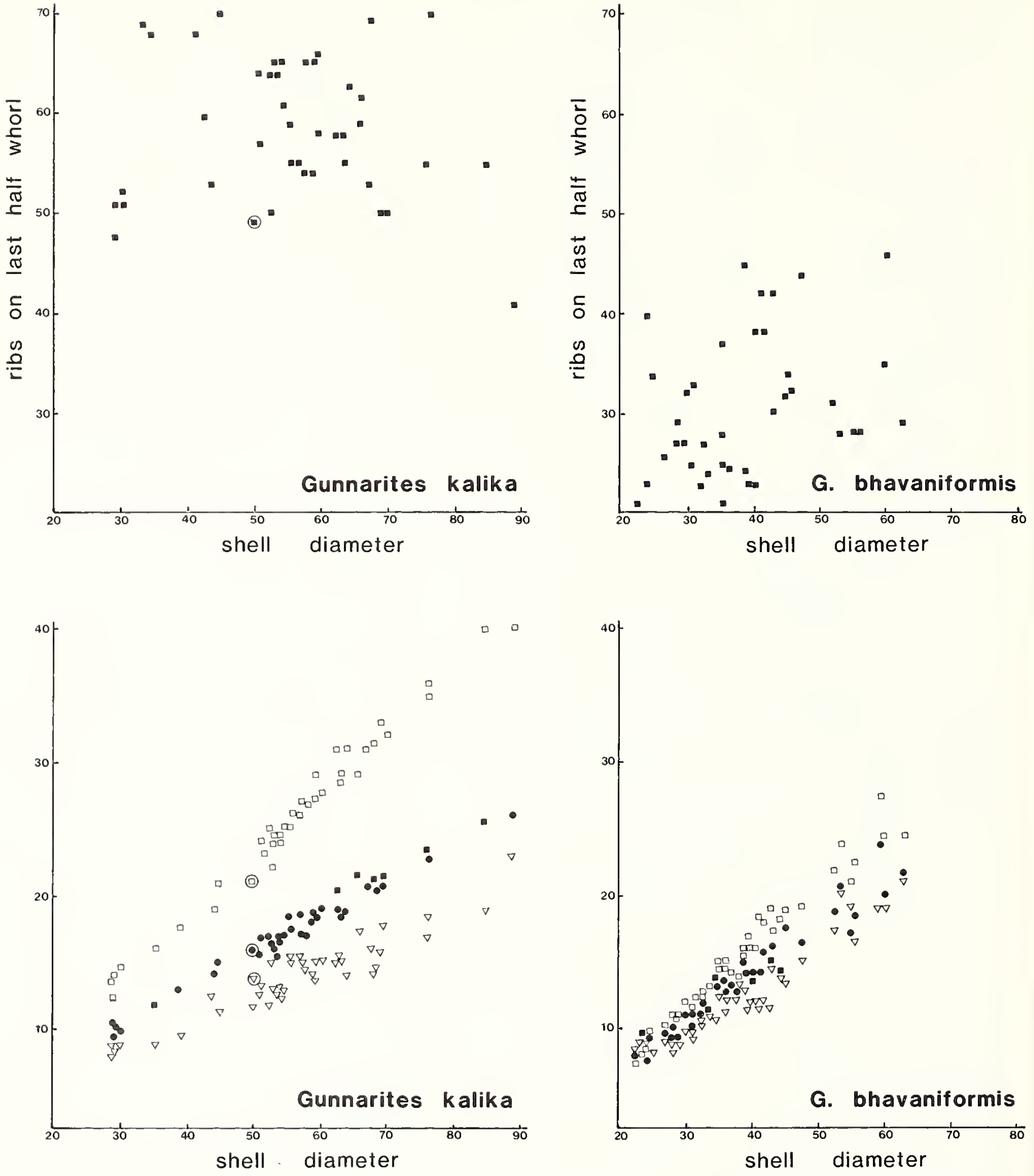
HENDERSON and McNAMARA, *Grossouvrites* and *Gunnarites*



TEXT-FIG. 8. Ribbing densities (upper) and shell measurements (lower) for *Gunnarites kalika* (Stoliczka) and *G. bhavaniformis* (Kilian and Reboul) inclusive of *G. kalika* Spath *non* Stoliczka. In the shell measurement plots squares represent whorl height, dots represent whorl breadth, and triangles represent umbilical width. Points representing the type specimen of *G. kalika* based on Stoliczka 1865, pl. 70, fig. 5*a*, *b*, are shown by symbols enclosed in a circle. Scales are in millimetres.

Constrictions number four to eight per whorl, becoming more numerous as the shell diameter increases; they are straight and prorsiradiate, each truncating one or two ribs. Suture, with E shallow, L deep and asymmetrically trifid, and U retracted on the umbilical wall, is typical of the genus.

Dimensions.

	D	H	B	B/H	U	%
WAM 81.2645	36·0	12·8	12·5	0·98	13·0	36
WAM 81.2542	38·5	14·0	13·5	0·96	14·0	36
WAM 83.2708	43·0	16·5	14·8	0·90	16·0	37
WAM 81.2513	86·0	34·0	27·0	0·79	28·0	33

Remarks. The marked reduction in rib density with growth characterizes this species and distinguishes it from other *Gunnarites*. *G. denticulatus* (Marshall), revised by Henderson (1970), somewhat resembles *G. raggatti* but its whorl profile with subparallel flanks is different, whorl compression begins later in ontogeny and is not marked, and the rib density increases during ontogeny rather than reducing. *G. varicostatus* Henderson (1970) has comparable shell dimensions but its inner whorls are much less densely ribbed.

G. raggatti may be present in Patagonia. The specimen incorrectly assigned to *G. kalika* Stoliczka by Blasco *et al.* (1980) shows the same ontogenetic reduction in rib density and appears to be indistinguishable from the Western Australian species in its other characteristics.

Genus KOSSMATICERAS de Grossouvre, 1901

Subgenus NATALITES Collignon, 1954

Kossmaticeras (*Natalites*) *brunnschweileri* sp. nov.

Plate 6, figs. 5, 6; Plate 7, figs. 2, 3, 5

Material. Holotype WAM 83.2709, locality 23. Paratypes WAM 81.2382, locality 4; WAM 83.1712, locality 16; WAM 83.2710, locality 23; WAM 83.2711, locality 25.

Description. Shell widely umbilicate with slightly depressed volutions up to a shell diameter of approximately 35 mm, thereafter becoming more involute with increasingly compressed volutions. Umbilical wall curves outwards to a well-defined umbilical shoulder; flanks are flattened and converge slightly to a well-rounded venter. In juvenile whorls up to a shell diameter of about 40 mm, there are some seven umbilical tubercles per half whorl. Each tubercle gives rise to two to three primary ribs with one to two additional primaries beginning from the umbilical shoulder between tubercles to make a total of twenty to twenty-five ribs per half whorl. More mature growth stages have seven to nine umbilical tubercles per half whorl and a similar arrangement of primary ribs. A few secondaries appear in the mid-flank region and the rib number increases to some thirty-five per half whorl for shell diameters of 60–85 mm. Ribs are thin and weakly flexuous, being prorsiradiate on the dorsal flanks, rectiradiate in the mid-flank area, and very weakly prorsiradiate across the ventral flanks and venter. Five prominent, straight prorsiradiate constrictions per whorl, each truncating two or three ribs. Suture complexly divided with E broad and not quite as deep as the trifid L; U is retracted on the umbilical shoulder and wall.

Dimensions.

	D	H	B	B/H	U	%
WAM 81.2382	34·0	11·2	12·0	1·07	15·0	44
WAM 83.2710	42·5	14·5	12·8	0·88	17·2	40
WAM 83.2709	68·5	27·5	20·5	0·74	22·8	33

Remarks. The holotype retains areas of well-preserved shell and shows the ribs to be non-crenulate. *K.* (*N.*) *brunnschweileri* is comparable with *Kossmaticeras* (*Natalites*) described from south-eastern Africa and recently revised by Kennedy and Klinger (in press) who treat the material as comprising a single, variable species for which *K.* (*N.*) *africanus* (van Hoepen 1920) has priority. The African species is distinguished from *K.* (*N.*) *brunnschweileri* by the more prorsiradiate course of its ribs, especially on the ventral flanks and venter, and its more sinuous constrictions.

Kossmaticeras (*Natalites*) sp. (juvenile)

Plate 7, figs. 4, 5

Material. One specimen, locality 23.

Description. Shell moderately involute with volutions overlapping by about 50%. Whorls compressed with an outwardly sloping umbilical wall, a clearly defined umbilical shoulder, weakly convex, convergent flanks, and a narrowly arched venter. Some fifteen umbilical bullae per whorl, each generally giving rise to two primary ribs with two or three additional primaries beginning from the umbilical shoulder between adjacent bullae. Sporadic secondaries appear in the mid-flank region so that in all there are some forty-five ribs on the last whorl. All the ribs are thin and separated by interspaces wider than themselves; they swing forward on the dorsal flanks, straighten at the mid-flank, and are very weakly projected across the venter. Five weakly flexuous, prorsiradiate constrictions per whorl, each bordered by collars and truncating three ribs. Suture typical of the Kossmaticeratidae with L deep and trifid and U retracted on the umbilical shoulder and wall.

Dimensions.

	D	H	B	B/H	U	%
WAM 83.2713	39·2	16·0	12·2	0·76	12·5	32

Remarks. The specimen is well preserved, retaining much of its shell. It appears to represent a new species of *Kossmaticeras* (*Natalites*), distinguished by its flexuous ribbing and compressed shell form, but more mature growth stages need to be documented before it can be formally named.

Genus MAORITES Marshall, 1926

Maorites densicostatus (Kilian and Reboul, 1909)

Plate 4, figs. 7, 8, 11–13

1909 *Madrasites bhavani* (Stoliczka) var. *densicostatus* Kilian and Reboul, p. 30, pl. 15, fig. 4; pl. 18, fig. 1.
1964 *Maorites densicostatus* (Kilian and Reboul); Leanza, pl. 1, figs. 6, 7.
1965 *Maorites densicostatus* (Kilian and Reboul); Howarth, p. 58, figs. 2*d*, *e*, 3c, d.
?1969 *Maorites subtilistriatus* Collignon; Collignon, p. 72, pl. 542, fig. 2124.
1977 *Maorites densicostatus* (Kilian and Reboul); Collignon, p. 11, pl. 1, fig. 3; pl. 5, fig. 1.
1980 *Maorites tenuicostatus* Marshall; Blasco *et al*., p. 488, pl. 14, fig. 1.

Material. Seventeen specimens, localities 6, 7, 12, 14–18, and 22.

Description. Shell compressed, quite strongly so from a diameter of some 40 mm where B/H is 0·64–0·70, and involute, with U measuring some 25% of the post-juvenile shell diameter. Umbilical wall steep but not quite vertical, reflected sharply at the umbilical shoulder into flattened flanks which converge slightly to a narrowly arched venter. Some twenty-six weakly developed, elongate umbilical bullae per whorl, extending down the umbilical wall from the shoulder almost to the umbilical seam. Each gives rise to two or three ribs and an additional rib begins from the shoulder between bullae. Intercalatory ribs, one after every two or three primaries, appear on the mid-flanks. Ribs are prorsiradiate and gently flexuous; they number 145–160 per whorl up to a shell diameter of 50–60 mm and thereafter become coarser and rather more widely spaced. Weakly flexuous, prorsiradiate ribs number six to ten per whorl and each truncates three or four ribs. They are margined

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EXPLANATION OF PLATE 6

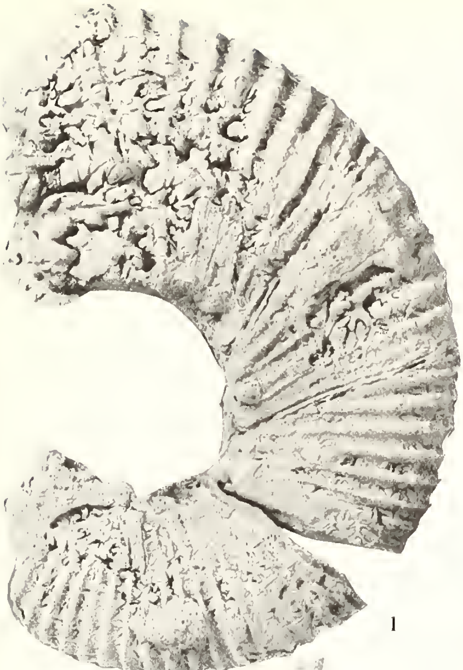
Figs. 1–4, 9–10. *Gunnarites raggatti* sp. nov. 1–2, paratype, WAM 81.2513, ×1. 3–4, paratype, WAM 81.2645, ×1. 9–10, holotype, WAM 81.2542, ×1.

Figs. 5–6. *Kossmaticeras* (*Natalites*) *brunnschweileri* sp. nov., paratype, WAM 81.2382, ×1.

Figs. 7–8. *Neograhamites carnarvonensis* sp. nov., holotype, WAM 80.840, ×1.

Figs. 11–14. *Brahmaites* (*Brahmaites*) *kossmati* sp. nov. 11–12, holotype, WAM 80.786, ×1. 13–14, paratype, WAM 82.3083, ×1.

PLATE 6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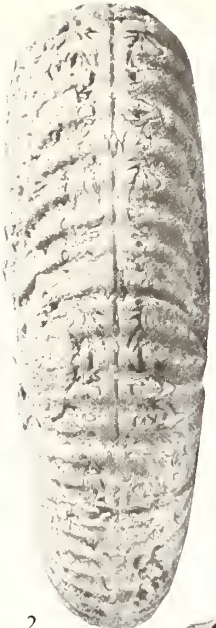
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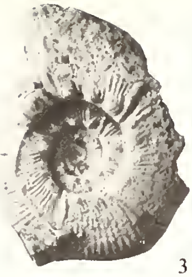
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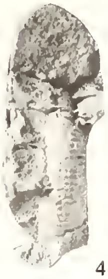
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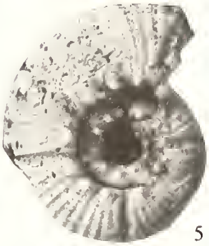
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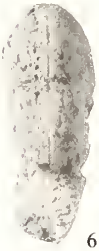
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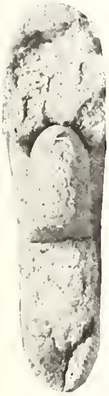
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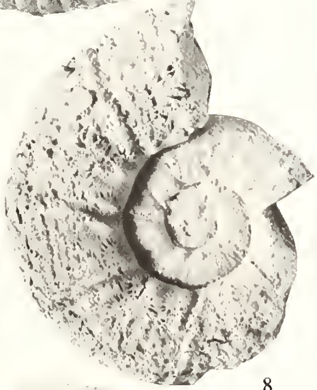
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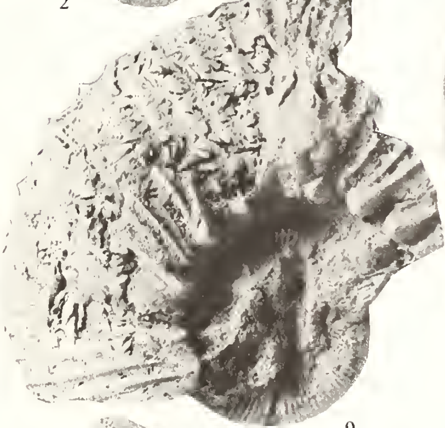
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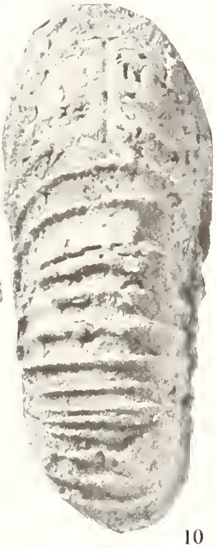
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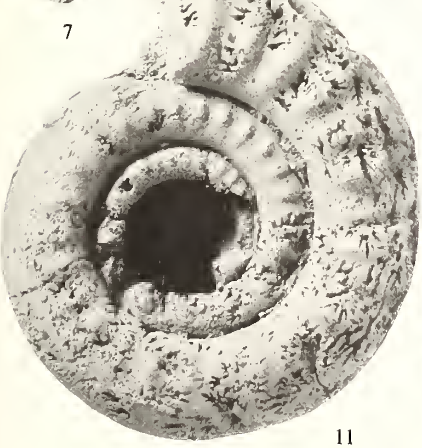
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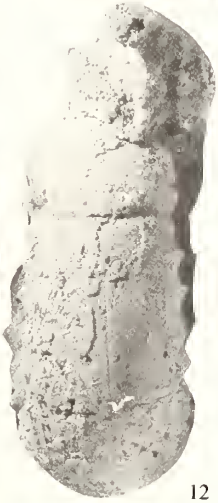
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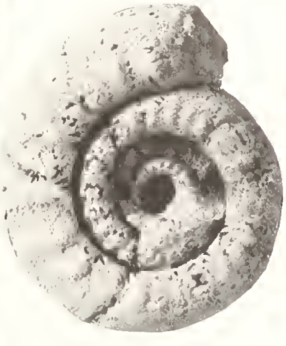
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HENDERSON and McNAMARA, Kossmaticeratidae by ridges, that on the adapical side being the strongest, and sometimes thickened on the umbilical shoulder and wall to form bullae additional to those which relate to the ribs. Suture typical of the genus, complexly divided even on juvenile shells.

Dimensions.

	D	H	B	B/H	U	%
WAM 81.2633	26·5	11·0	8·5	0·77	8·0	30
WAM 81.2633	37·0	15·5	11·0	0·71	9·5	26
WAM 80.847	45·0	19·0	13·0	0·68	11·5	25
WAM 80.1000	53·0	22·5	15·0	0·67	13·0	25
WAM 81.2613	55·0	24·0	15·5	0·64	14·0	25

Remarks. The present specimens compare very well with Antarctic Peninsula *M. densicostatus* described by Kilian and Reboul (1909), Spath (1953), and Howarth (1966). Although they are all immature, several show the beginnings of the somewhat coarser ribbing which characterizes *densicostatus* and sets it apart from *M. tenuicostatus* (Marshall) (= *M. suturalis* Marshall) (see Henderson 1970, p. 51). As noted by Howarth (1966), *M. subtilistriatus* Collignon may perhaps be a synonym of *M. densicostatus*. The two species agree in all characteristics, except that *subtilistriatus* has fractionally less compressed whorls (B/H of 0·7–0·74 at shell diameters exceeding 100 mm) than *densicostatus*. Poorly preserved *Maorites* resembling *subtilistriatus* are recorded from southern Africa by Kennedy and Klinger (in press).

A close morphological similarity between *M. densicostatus* and finely ribbed *Gunnarites bhavaniformis* Kilian and Reboul (= *G. kalika* Spath *non* Stoliczka) was observed by Spath (1953) and Howarth (1966) for Antarctic Peninsula material. In the Western Australian collections, *M. densicostatus* and *G. kalika* (Stoliczka) are indistinguishable in shell dimensions, whorl profile, and the density of ribbing. Save for rib crenulation, which is indeterminable for many specimens due to imperfect shell preservation, individuals of the two species can only be separated by the nature of umbilical bullae which are consistently much stronger and less elongate in *G. kalika*.

It is tempting to suggest that *M. densicostatus* was derived from a finely ribbed *Gunnarites* like *G. kalika*, in Campanian time, by the loss of rib crenulation and slight modification to the ornament. However, *Maorites* (including *M. subtilistriatus*) were already speciated in the lower Campanian of Madagascar (Collignon 1955b, 1969). It may be that finely ribbed, compressed kossmaticeratids were derived from more than one ancestral stock and that *Maorites* is a polyphyletic grouping.

Genus GROSSOUVRITES Kilian and Reboul, 1909

Grossouvrites gemmatus (Huppé, 1854)

Plate 5, figs. 1–7

1854 *Ammonites gemmatus* Huppé, in Gay, p. 35, pl. 1, fig. 3.
1958 *Grossouvrites gemmatus* (Huppé); Howarth, p. 12, pl. 2, fig. 4*a*, *b*.
1965 *Grossouvrites gemmatus* (Huppé); Hünicken, p. 77, pl. 6, figs. 1, 2; pl. 7, figs. 8, 9.

Material. Eighteen specimens, localities 5, 9, 12, 15–20, 23, and 25.

Description. Juvenile growth stages, up to a shell diameter of about 30 mm, are evolute, the umbilicus measuring about 35% of the shell diameter, and have an equidimensional whorl profile. Later growth stages become involute, the umbilicus reducing to some 26% of the shell diameter, and are slightly compressed. Umbilical wall steep but not vertical, sharply turned at the umbilical shoulder into weakly convex flanks which converge slightly towards a broadly rounded venter. There are some twenty-two small, regularly spaced umbilical tubercles per whorl, each giving rise to one or two ribs, with an additional rib beginning at the umbilical shoulder between tubercles. Secondary ribs, one after each primary, begin from the mid-flank region so that about 100 ribs are present on each whorl. Primaries have a slight prorsiradiate inclination on the dorsal flanks but, like the secondaries, are straight and rectiradiate on the ventral flanks and very weakly projected on the venter. Constrictions are restricted to juvenile growth stages with shell diameters of less than 35 mm. Each is margined on both sides by collars, that on the adapertural side being slightly the stronger. They are almost straight with a slightly prorsiradiate inclination on the flanks and weakly projected on the venter; each truncates one or two ribs. The suture is very fine divided, even at juvenile growth stages at shell diameters less than 10 mm, unusually so for a kossmaticeratid. L is deeper than E and trifid; U is retracted and on the umbilical wall.

Dimensions.

	D	H	B	B/H	U	%
WAM 81.2634	30·0	12·0	12·0	1·00	10·5	35
WAM 10574	44·5	19·0	16·5	0·87	13·5	30
WAM 81.2521	55·0	25·0	19·5	0·78	15·0	27
WAM 83·2690	64·5	31·2	24·8	0·79	16·8	26
BM C49087	*c.* 66·0	34·8	28·0	0·80	16·8	*c.* 25
WAM 83.2689	91·0	41·0	29·8	0·73	22·5	25
WAM 83.2691	100·5	44·0	31·5	0·72	25·5	25

Remarks. The Western Australian specimens are identical in shell dimensions and other characters with the Antarctic Peninsula specimen (BM C49087) figured by Howarth (1958) and the original of Kilian and Reboul's 1909, pl. 17, fig. 2*a*, *b* of which the British Museum (Natural History) holds a cast (C23232). The type specimen illustrated by Huppé is a little more compressed with a whorl breadth/whorl height ratio of about 0·76 at a shell diameter of about 40 mm. However, the specimens measured by Steinmann (1895) and Hünicken (1965) are considerably more compressed with whorl breadth/whorl height ratios of 0·61 and 0·51 respectively; presumably they are crushed.

The large fragment of body chamber figured by Spath (1953, pl. 5, fig. 1*a*, *b*) shows that the same style of ornament persists to a late stage of growth where the shell diameter is more than 180 mm.

Genus BRAHMAITES Kossmat, 1897
Subgenus BRAHMAITES

1897*a* *Brahmaites* Kossmat, p. 44.

Type species. Ammonites brahma Forbes, 1846, p. 100, pl. 8, fig. 1.

Remarks. Brahmaites of current interpretation comprises a loosely knit group of Maastrichtian kossmaticeratids characterized by evolute shells with inflated whorls lacking a clear umbilical shoulder and with ribbing effaced or absent, at least in early growth stages. Siphonal tubercles are present at late growth stages.

The type species, *B. brahma* (Forbes) from Pondicherry, southern India, is represented by a substantial suite of specimens held by the British Museum (Natural History), including Forbes's type series. All growth stages are represented, to a shell diameter of 108 mm. The whorls are depressed throughout ontogeny, strongly so when juvenile where the whorl breadth/whorl height ratio ranges up to 2·04. Ornament consists of numerous umbilical bullae which disappear at a shell diameter of about 70 mm, annular ribs that first appear at a shell diameter of about 60 mm, and infrequent constrictions preceded by prominent collars which bear siphonal tubercles at a late stage of growth. A closely related species, *B. kossmati* sp. nov., is established below for Western Australian material. Specimens from Madagascar described by Collignon (1938, 1971), and from Otacod, southern India, described by Kossmat (1897*a*) were originally referred to *B. brahma* but may represent other species. All of these forms comprise a closely related species group whose geographic range was restricted to the Indian Ocean.

A second species group may be recognized, of which the southern Indian *B. vishu* (Forbes) is the best-known example. This species has equidimensional to weakly compressed whorls bearing simple annular ribs which are weak on initial growth stages but become widely spaced and strong, with siphonal tubercles, later in ontogeny. Umbilical tubercles are lacking. Included here is the French *B. haugi* (Seunes, 1891) (= *Gaudryceras planorbiforme* Grossouvre, 1894, *non* Böhm 1891), *B. sachalinensis* Yabe and Shimizu, 1924 from Saghalien, and probably *B. nikobokensis* Collignon, 1971 from Madagascar. Additional records are of *B. vishnu* from Armenia (Atabekian and Akopian 1970) and *B. haugi* from Madagascar (Collignon 1938). Besides a different morphology, this species group has a much wider distribution than *Brahmaites* (*s.s.*). It seems worthy of subgeneric segregation for which *Anabrahmaites*, with *A. vishnu* (Forbes) as its type species, has already been introduced by Yabe and Shimizu (1924, p. 79).

The juvenile *B. haugi* (Seunes), recorded from Spain by Wiedmann (1969, pl. 3, fig. 4), is too small and poorly preserved to be given a generic assignment and *B. rotundus* Marshall, 1926 is now known to be a juvenile *Jacobites* (*J.*) *nodulosus* (Marshall) (see Henderson 1970, p. 42).

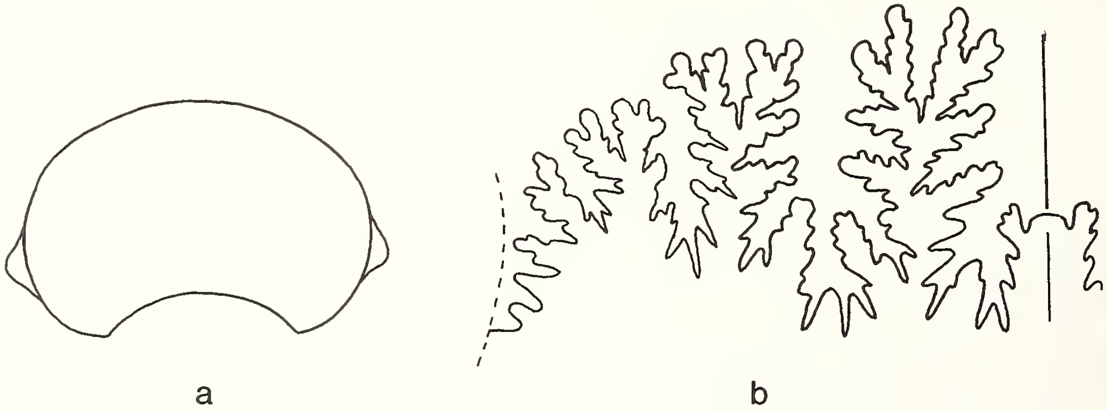
Brahmaites (*Brahmaites*) *kossmati* sp. nov.

Plate 6, figs. 11–14; Plate 7, fig. 1; text-figs. 9*a*, *b*, 10

?1897*a* *Brahmaites brahma* (Forbes); Kossmat, p. 45 *pars*, pl. 8, fig. 7*a*, *b*

Material. Holotype WAM 80.786, locality 10. Paratypes WAM 82.3083, locality 5; WAM 80.964, 83.2697, 83.2700, locality 12; WAM 83.2698, 83.2699, locality 25.

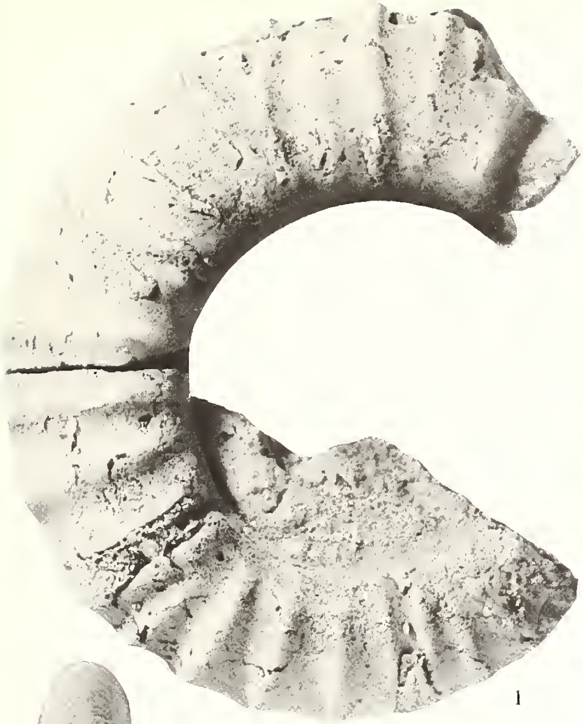
Description. Shell serpenticonic with the umbilicus measuring about 50 % of the shell diameter. Whorls strongly depressed with a B/H ratio of 1·6–1·8 at a shell diameter of 50 mm, increasing to more that 2·0 in the initial growth stages. Convex, outwardly sloping umbilical wall merges imperceptibly with convex flanks so that no umbilical shoulder is defined; the venter is broadly arched. Prominent, radial umbilical bullae number twenty-two to twenty-six per whorl. Up to a shell diameter of 55 mm they extend for a short distance on to the flanks but at later growth stages, up to a shell diameter of approximately 70 mm, they extend further, reaching across the flanks to the edge of the venter. For a final growth stage the ribs continue their rectiradiate course across the venter and become much stronger. Here they merge imperceptibly with the umbilical bullae and some lack bullae completely. Irregularly spaced constrictions, numbering three to five per whorl, are rectiradiate on the umbilical wall, swing gently forward on the flanks, and are projected on the venter. They are bordered by collars of which the strongest is that positioned adapically which develops a siphonal tubercle at a shell diameter of approximately 70 mm. Suture of kossmaticeratid plan but not complexly divided. L is asymmetrically trifid and only slightly deeper than E, U is retracted on the umbilical wall, and I is trifid.



TEXT-FIG. 9. *Brahmaites kossmati* sp. nov. *a*, whorl profile, paratype, WAM 80.964, × 2. *b*, suture, holotype, WAM 80.786, × 4.

EXPLANATION OF PLATE 7

Fig. 1. *Brahmaites* (*Brahmaites*) *kossmati*, sp. nov., paratype, WAM 83.2697, × 1.
Figs. 2–3. *Kossmaticeras* (*Natalites*) *brunnschweileri* sp. nov., holotype, WAM 83.2709, × 1.
Figs. 3, 4. *Kossmaticeras* (*Natalites*) sp. juv., WAM 83.2713, × 1.
Fig. 5. *K.* (*N.*) *brunnschweileri*, paratype, WAM 83.2710, × 1.
Fig. 6. *Pachydiscus* (*Pachydiscus*) *neubergicus dissitus* subsp. nov., holotype, WAM 83.2694, × 1.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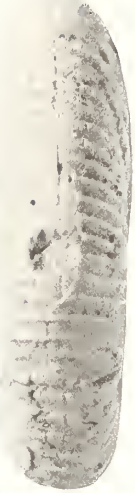
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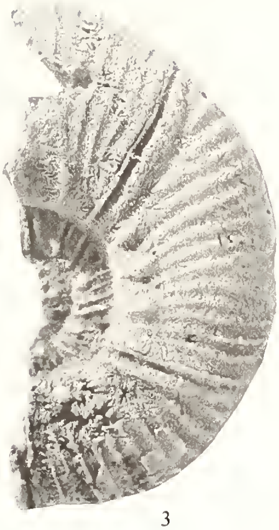
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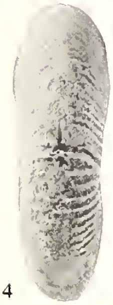
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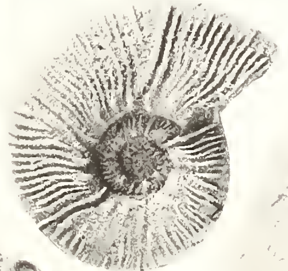
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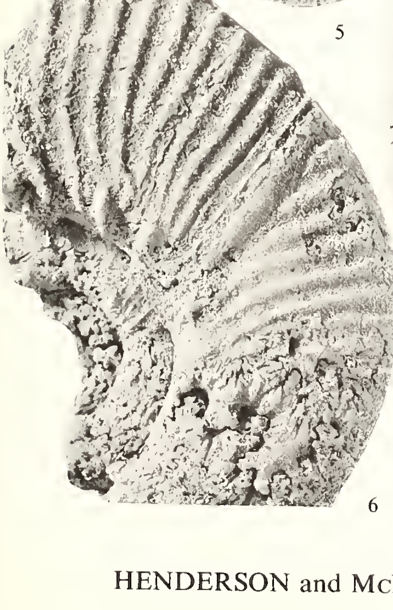
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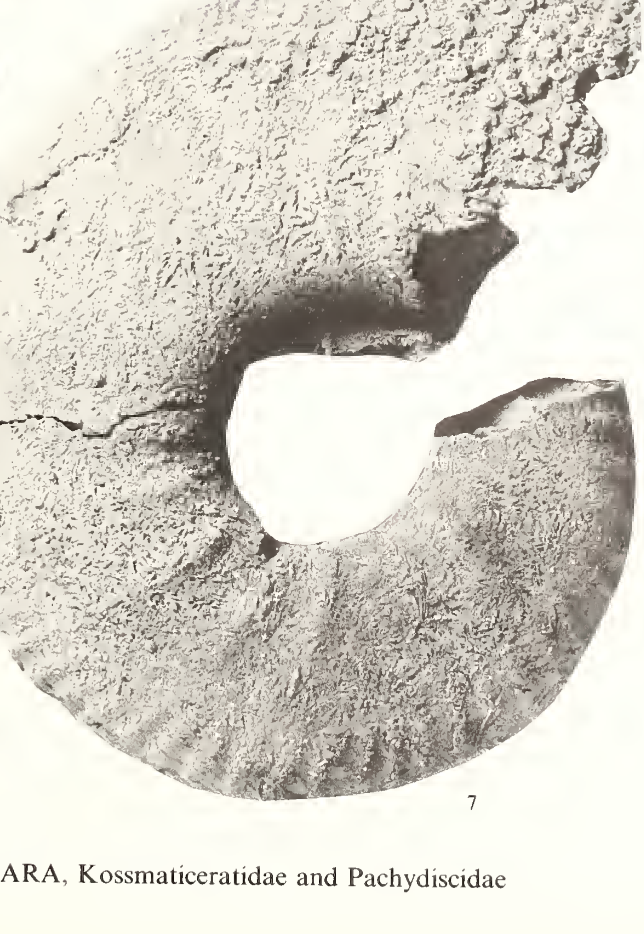

7

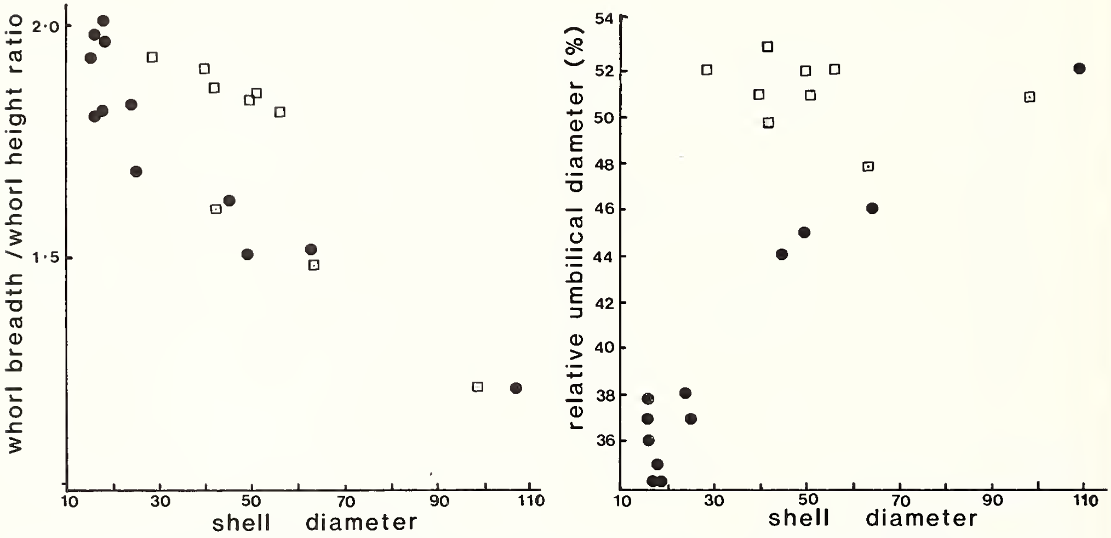
HENDERSON and McNAMARA, Kossmaticeratidae and Pachydiscidae

Dimensions.

	D	B	H	B/H	U	%
WAM 81.3083	28·0	14·0	7·2	1·94	14·5	52
WAM 80.964	40·0	18·0	9·5	1·90	20·5	51
WAM 81.3083	42·0	19·0	10·2	1·86	22·2	53
WAM 83.2700	42·2	19·0	11·8	1·61	21·0	50
WAM 80.964	50·0	23·0	12·5	1·84	26·0	52
WAM 80.786	51·0	18·5	10·0	1·85	26·0	51
WAM 80.786	56·0	24·5	13·5	1·81	29·0	52
WAM 83.2698	62·8	26·0	17·5	1·49	30·0	48
WAM 83.2697	98·8	36·5	29·8	1·22	50·5	51

Remarks. WAM 83.2697 probably represents a mature specimen as it has three-quarters of a whorl of body chamber terminated by a prominent constriction. None of the specimens shows the inception of the adult ornament but its development is almost certainly gradual with the ribs extending progressively further across the flanks and on to the venter.

B. (*B.*) *kossmati* is closely related to *B. brahma* (Forbes). Juveniles of *kossmati* are distinguished by being more widely umbilicate and tend to have more depressed volutions (text-fig. 10). When adult, *kossmati* has stronger, more numerous ribs than its Indian ally.



TEXT-FIG. 10. Plots of whorl breadth/whorl height and umbilical diameter expressed as a percentage of the shell diameter showing ontogenetic trends for *Brahmaites* (*B.*) *brahma* (Forbes) (dots) and the separation of *Brahmaites* (*B.*) *kossmati* sp. nov. (squares). Abcissa scales are in millimetres.

The status of the two specimens from Otacod, southern India, figured by Kossmat (1897*a*, pl. 8, figs. 7*a*, *b*, 8*a*–*c*) as *B.* (*B.*) *brahma*, is uncertain. The ribbed juvenile is definitely not of this species as several of the British Museum (Natural History) juveniles from the type series of *brahma* retain their shell and show the test surface to be smooth. The larger specimen, with a shell diameter of 88 mm, appears to be more like *B.* (*B.*) *kossmati* in shell form and in ornament but does not develop the mature ribbing. The status of *B.* (*B.*) *brahma* recorded by Collignon (1938, 1971) is also in doubt. Collignon's measurements show the Madagascan specimens to be much more slender whorled than the Pondicherry types, with whorl breadth/whorl height ratios of about 1·2 at shell diameters of 50–80 mm. Perhaps they represent a local species, but it may be noted that a Pondicherry specimen measured by Stoliczka (1865) was reported as being equally slender whorled.

Whereas adult kossmaticeratids as a whole tend to be involute with equidimensional or compressed whorl profiles, the evolute coiling and depressed whorl profile shown by *B.* (*B.*) *kossmati* and *B.* (*B.*) *brahma* are typical of many juveniles. For example, measurements of ontogenetic series for New Zealand kossmaticeratids show this trend for *J.* (*J.*) *nodulosus* (Marshall) and *Gunnarites spathi* Henderson (see Henderson 1970). Indeed a juvenile of the former was mistakenly referred to *Brahmaites* by Marshall (1926). Effacement and eventual loss of ornament and simplification of the suture is typical of kossmaticeratids, like all ammonites, as the initial whorls are followed back towards the apex. It may well be that *Brahmaites* (*Brahmaites*) is the Maastrichtian result of paedomorphic derivation from a more typical Campanian kossmaticeratid stock.

Genus NEOGRAHAMITES Spath, 1953

Type species. Neograhamites kiliani Spath, 1953.

Remarks. Neograhamites is characterized by an evolute shell form with a low, outwardly sloping umbilical wall, subdued ornament of umbilical tubercles, and straight, rectiradiate ribs except for a final stage of growth where coarse ribs prevail. It is closely allied to *Pseudokossmaticeras* Spath 1922, from which it differs only in having fewer, more distinct umbilical tubercles to which ribs join in pairs rather than singly. The late growth stage coarsening of the ribs displayed by *N. kiliani* is also shown by some *Pseudokossmaticeras*—for example, *P. galicianum* (Favre) as figured by Błaszkiewicz (1980, pl. 54, fig. 1).

In addition to the type species, *N. taylori* Spath also from the Antartic Peninsula was included in the genus at its establishment, and a further species, *N. transitorius* Henderson (1970) added from New Zealand. However, both of these species are much more involute than *N. kiliani* or *N. carnarvonensis* from Western Australia (established herein), with higher, steeper umbilical walls and strong umbilical tubercles. The same observations are true for the Patagonian specimens described by Blasco *et al.* (1980) as *Neograhamites* aff. *taylori* Spath. *N. transitorius* is more satisfactorily placed in *Kossmaticeras* (*Natalites*) Collignon, 1955*b* whereas the somewhat effaced ribbing on the dorsal flanks of *N. taylori* suggests reference to *Kossmaticeras* (*Karapadites*) Collignon, 1954.

Holcodiscus hauthali Paulcke (1906) was compared with *Neograhamites* by Matsumoto (1955) and by Theidig and Wiedmann (1976). It presumably is the basis of the record of *Neograhamites* from Patagonia given by Arkell, Kummel and Wright (1957). Leanza (1967) referred this species to *Pseudokossmaticeras*. However, its degree of involution, steep umbilical wall, and flexuous ribs show that it is not closely related to either of these genera. It resembles *N. transitorius* Henderson and should likewise be transferred to *Kossmaticeras* (*Natalites*).

Neograhamites as interpreted here comprises but two species, and is known only from the Antarctic Peninsula and Western Australia. Its range is ?upper Campanian–Maastrichtian.

Neograhamites carnarvonensis sp. nov.

Plate 6, figs. 7, 8

Material. Holotype WAM 80.840, locality 9.

Description. Shell discoidal, evolute, with compressed whorls. Umbilical wall low, vertical at the umbilical seam but convex and sloping outwards to pass smoothly into the flanks such that the umbilical shoulder is rather poorly defined. The flanks are somewhat flattened and very slightly convergent, the venter narrowly rounded. Six or seven straight, prorsiradiate constrictions per whorl, bordered by collars which are sometimes raised into very weak bullae as they cross the umbilical shoulder. Some nine stronger umbilical bullae per whorl lying between the constrictions are not as well marked on the last whorl as on that preceding it. Some thirty-six straight, rectiradiate ribs per whorl, most arising in pairs from the umbilical bullae or from the umbilical wall between tubercles. Two ribs preceding each constriction are truncated. Suture kossmaticeratid in style and quite complexly divided. L is considerably deeper than E, which is asymmetrically trifid; U is retracted on the umbilical wall.

Dimensions.

	D	H	B	B/H	U	%
WAM 80.840	49·0	16·5	13·5	0·82	20·0	41

Remarks. N. carnarvonensis compares closely with *N. kiliani* Spath (1953), differing only in having a more compressed whorl section with subparallel flanks and a broadly rounded venter. The unique holotype of the Antarctic species, BM C41366, has a whorl breadth/whorl height ratio of 0·94. Even weakening of the umbilical tubercles at a shell diameter of 35–40 mm is a shared feature. The change in ornament to sparse, coarse ribs shown by *N. kiliani* occurs at a shell diameter of some 55 mm and represents a later stage of growth than those shown by the holotype of *N. carnarvonensis.*

Family PACHYDISCIDAE Spath, 1922
Genus PACHYDISCUS Zittel, 1884

1884 *Pachydiscus* Zittel, p. 466.
1900 *Parapachydiscus* Hyatt, p. 570.
1958 *Joaquinites* Anderson, p. 218.

Type species. Pachydiscus (*P.*) *neubergicus* (von Hauer, 1858).

Remarks. Pachydiscus is an important genus for Campanian and Maastrichtian correlation whose potential has not been fully realized due to inadequate knowledge of its species. Most records of the genus have been based on a small number of specimens for which a full ontogeny cannot be documented nor intraspecific variation determined. In addition, several important species were first described in the middle of the last century and were based on inadequate types, illustrated by hand, and their type series have not as yet been adequately revised. As a result. the classification of *Pachydiscus* species, especially those from Europe, is perhaps less well understood than that of any other upper Cretaceous genus. The three Western Australian species are all present in Europe and are represented by sufficient material to permit a substantially complete documentation of their morphology, thereby resolving some of the conflict in the European literature.

In contrast to the other two species, generic placement of *P. fresvillensis* Seunes is somewhat arbitrary. Its depressed immature volutions and relatively coarse ribbing suggest reference to *Eupachydiscus* Spath, 1922, but its weakly compressed adult whorls with flattened, convergent flanks and the eventual restriction of ribbing to the ventral flanks and venter are characteristics of *Pachydiscus*. It is retained in *Pachydiscus*, thereby conforming with the previous literature. Two subgenera are recognized within *Pachydiscus*, distinguished by the nature of mature ornament. *Pachydiscus* (*Pachydiscus*) retains ribbing whereas it is lost from late growth stages of *P.* (*Neodesmoceras*) Matsumoto, 1947.

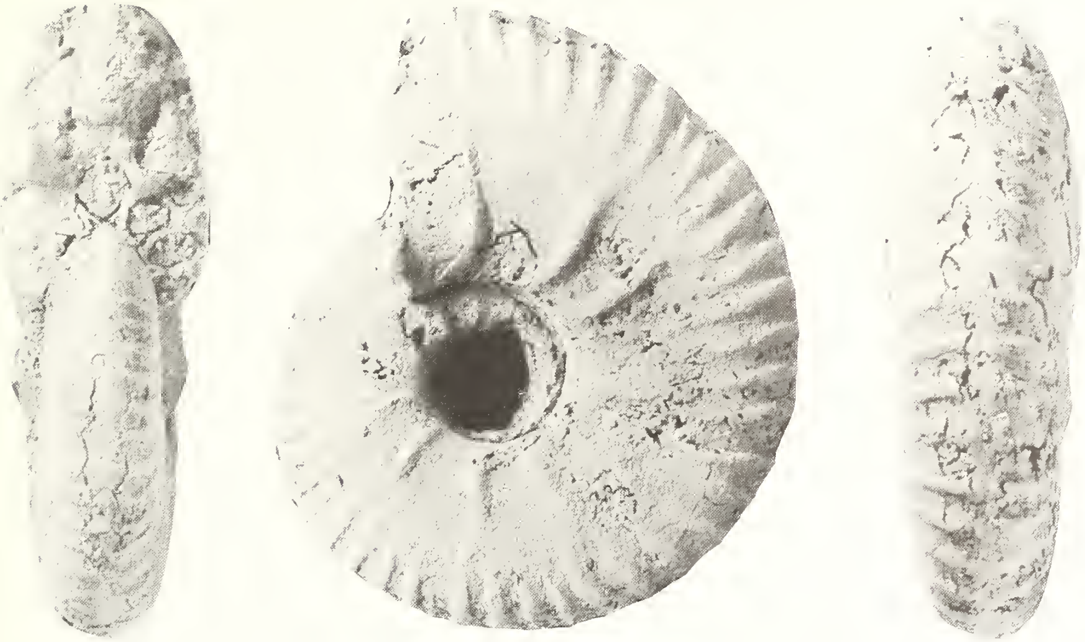
Subgenus PACHYDISCUS
Pachydiscus (*Pachydiscus*) *neubergicus dissitus* subsp. nov.

Plate 7, figs. 7, 9; Plate 10, figs. 3–6; text-figs. 11, 12*c*, 13*c*

1941 *Pachydiscus* aff. *gollevillensis* (d'Orbigny); Spath, p. 45, pl. 2, fig. 1*a*, *b*.

Material. Holotype WAM 83.2694, locality 15. Paratypes UWA 20139, WAM 60.105, locality 1; WAM 81.2555, locality 5; WAM 60.54, 60.75g, 71.210, 80.838, locality 7; WAM 80.963, locality 12; WAM 81.2540, 83.2695, locality 16; WAM 83.2696, locality 17. Six additional specimens, localities 12, 16, 17, and 25.

Description. Shell compressed and involute, with a whorl breadth/whorl height ratio of 0·75–0·78 and an umbilicus which measures 26–28 % of the shell diameter. Umbilical wall inclined outwards, turning gently at the umbilical shoulder into weakly convex, slightly convergent flanks. Venter narrow, evenly rounded. Primary ribs, numbering about eleven per whorl, begin at a shell diameter of some 25 mm and extend from the umbilical seam to the mid-flanks. They are faint and rursiradiate on the umbilical wall but become rectiradiate on the dorsal flanks where they swell to form elongate umbilical bullae. Secondary ribs, confined to the ventral flanks and venter, begin at a shell diameter of 40–45 mm. They number twenty-three to twenty-five per half whorl up to a



TEXT-FIG. 11. *Pachydiscus* (*Pachydiscus*) *neubergicus dissitus* subsp. nov., paratype, WAM 81.2555, × 1.

shell diameter of 85–95 mm, thereafter becoming much more closely spaced and a little weaker. Their course is almost straight and slightly prorsiradiate, and they become generally stronger across the venter except on the mid-ventral line where they are slightly effaced. Some primary ribs are out of phase with the secondaries, being separated from them by a slight mid-flank gap. Suture typical of the genus, with U strongly retracted on the umbilical wall.

Dimensions.

	D	H	B	B/H	U	%
WAM 81.2540	43·2	18·5	14·2	0·76	11·2	26
WAM 60·75g	49·0	21·0	15·8	0·75	12·5	26
WAM 80.963	56·5	24·0	18·8	0·78	15·0	27
WAM 60.105	66·0	28·0	21·0	0·75	18·5	28
WAM 71.210	80·0	33·0	25·2	0·76	21·2	27
WAM 83.2696	92·8	40·0	29·2	0·73	25·5	27
WAM 83.2694	122·5	51·5	37·0	0·72	32·2	26

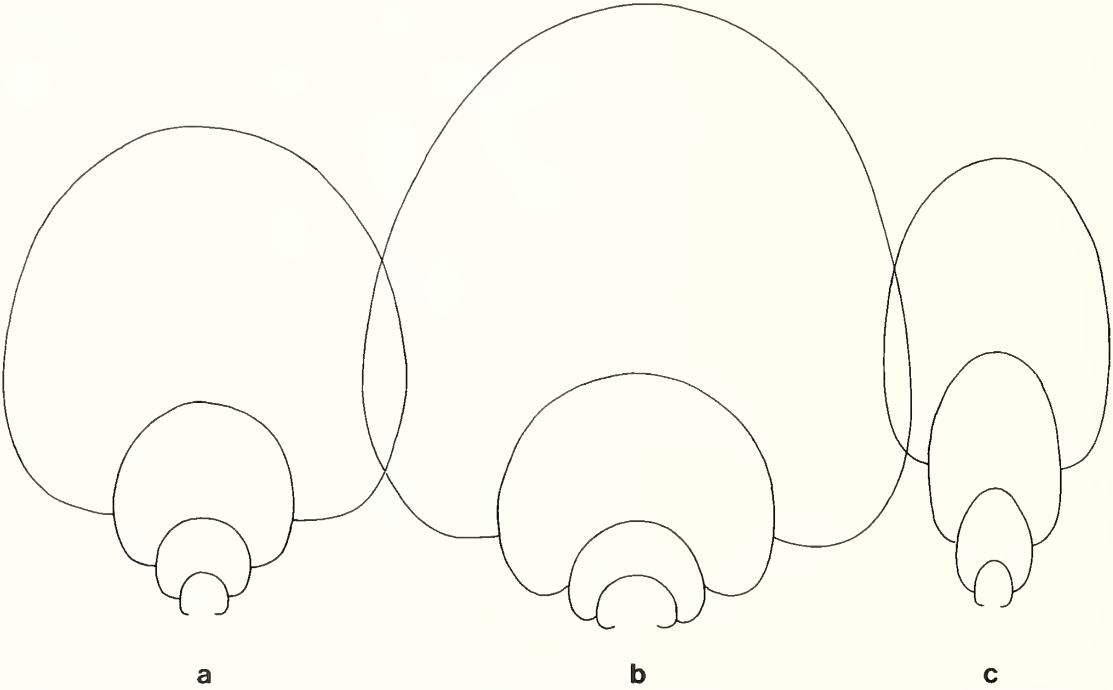
Remarks. The growth stage at which the fine, mature ornament first appears is somewhat variable. It commences at a shell diameter of 95 mm on the holotype (WAM 83.2694), but is absent from WAM 83.2696 at an equivalent diameter which represents the last preserved growth stage of that specimen. On UWA 20139, the specimen figured by Spath (1941, pl. 2, fig. 1*a*, *b*), fine ribbing appears at a shell diameter of 85 mm. Mature secondary ribs number about twenty-five per quarter whorl. The holotype consists entirely of phragmocone so that the adult ornament must have characterized most of the last whorl of a complete, fully grown shell.

P. (*P.*) *neubergicus* (von Hauer) is here regarded as a synonym of *P.* (*P.*) *chrishna* (Forbes). Separation of these two species is no doubt largely due to the original hand-drawn illustrations, those of Forbes (1846, pl. 9, fig. 2*a*, *b*) accentuating effacement of ornament on *chrishna* whereas those of von Hauer (1858, pl. 2, figs. 1–3) displayed *neubergicus* as having strong ornament. A comparison of the unique holotype of *chrishna* (BM C51041) with photographs of the type series of *neubergicus* (W. J. Kennedy, unpublished) shows the distinction to be much more subtle than the original illustrations suggest. The photographs of the *neubergicus* types and the holotype of *chrishna* show a change to mature ornamentation at a shell diameter of 8–9 cm where secondary ribs disappear and the primaries extend across the flanks to the margin of the venter, the bullae becoming more elongated and less clearly defined. A large French specimen of *neubergicus* figured by de Grossouvre (1894, pl. 30, fig. 4*a*, *b*) has similar adult ornament except that the primary ribs strengthen and become more widely spaced.

The synonymy of *P.* (*P.*) *neubergicus* (von Hauer 1858) and *P.* (*P.*) *chrishna* (Forbes 1846) cannot be satisfactorily resolved by application of the rule of priority. The name *neubergicus* is entrenched in the literature, having been used for this species in descriptions and lists from many European localities. It has, in addition, been used as the name of a lower Maastrichtian zonal index species for nearly ninety years. In contrast no specimens other than Forbes's unique holotype have been described or listed as *P.* (*P.*) *chrishna*. In consequence, Henderson and Kennedy (in press) have applied to the International Commission on Zoological Nomenclature to suppress *chrishna* in favour of *neubergicus*.

The Western Australia suite is assigned to a new subspecies, *P.* (*P.*) *neubergicus dissitus*, because its mature ornament is different from that of von Hauer's type series of *neubergicus* (*s.s.*) and other specimens referred to the species. Its earlier growth stages, however, are indistinguishable from European *neubergicus*, such as those illustrated by Schlüter (1872) and Błaszkiewicz (1980), and differ from Forbes's original of *chrishna* only in displaying slightly stronger ribs.

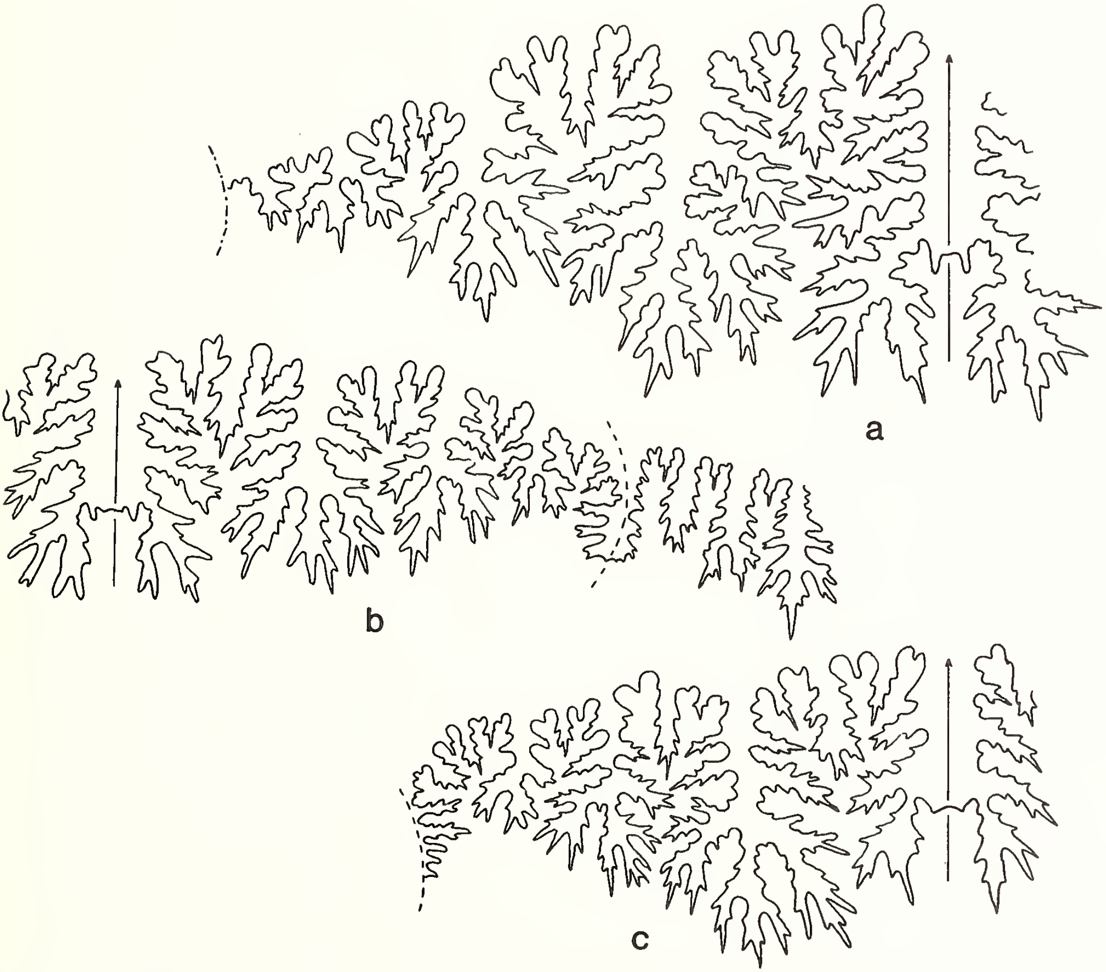
P. (*P.*) *neubergicus dissitus* may be regarded as a morphological intermediate between *neubergicus* (*s.s.*) and *P.* (*P.*) *gollevillensis* (d'Orbigny, 1850). These two species differ only in the density of secondary ribs, which number sixty to seventy per whorl for *gollevillensis* compared with forty-five to



TEXT-FIG. 12. Whorl profiles of *Pachydiscus* (*Pachydiscus*). *a*, *P.* (*P.*) *jacquoti australis* subsp. nov., drawn from paratypes WAM 81.2454 and WAM 81.2529. *b*, *P.* (*P.*) *fresvillensis* Seunes, WAM 2527, *c*, *P.* (*P.*) *neubergicus dissitus* subsp. nov., drawn from paratypes WAM 80.963 and WAM 81.2555. All ×1.

fifty per whorl for *neubergicus*. They have been often confused in the literature and Atabekian and Akopian (1969) considered them as subspecies of *gollevillensis* (*s.l.*). The mature ornament of *P.* (*P.*). *neubergicus dissitus* is very similar to that of *gollevillensis* (see Pl. 7, fig. 7; Pl. 9, figs. 5, 6) and evolution of the former to the latter could have been effected by accelerating the onset of fine secondary ribbing to an earlier stage of ontogeny.

P. perfidus de Grossouvre (1894, p. 213, pl. 34, fig. 1) has inner whorls like those of *P. neubergicus* but the adult ornament consists of coarse primaries which are strongly marked on the venter where they are separated by occasional intercalated secondaries of equal strength. Polish specimens referred to a new subspecies of *P.* (*P.*) *neubergicus*, *P.* (*P.*) *neubergicus raricostatus*, and to *P. perfidus* by Blaszkiewicz (1980) have similar adult ornament, as does the specimen figured by de Grossouvre (1894, pl. 38, fig. 3) as *P. neubergicus*. The status of these forms is equivocal because no reliable shell dimensions have been published, save for a whorl profile drawn by de Grossouvre (1894, superimposed on pl. 38, fig. 3) which suggests a whorl breadth/whorl height ratio of 0·9.



TEXT-FIG. 13. Sutures of *Pachydiscus* (*Pachydiscus*). *a*, *P.* (*P.*) *fresvillensis* Seunes, WAM 80.785. *b*, *P.* (*P.*) *jacquoti australis* subsp. nov., paratype, WAM 81.2352. *c*, *P.* (*P.*) *neubergicus dissitus* subsp. nov., paratype, WAM 60.105. All ×3.

P. (*P.*) *neubergicus* has been widely regarded as an index species of the lower Maastrichtian in Europe (see, for example, Arkell, Kummel and Wright 1957; Wiedmann 1979). It also occurs in the Maastrichtian of Armenia and India as well as in Western Australia.

Pachydiscus (*Pachydiscus*) *jacquoti australis* subsp. nov.

Plate 8, figs. 1, 2, 7–10; text-figs. 12*a*, 13*b*, 14, 15*a*

1941 *Pachydiscus* sp. nov.? Spath, p. 46.

Material. Holotype WAM 80.1004, locality 12. Paratypes WAM 81.2431, 81.2454, 81.2352, locality 4; WAM 81.2525, 81.2529, 82.3082, locality 5; WAM 71.213, 81.2708, 81.2711, NMV P31024, locality 6; WAM 60.76f, locality 7; WAM 80.827, 80.836, locality 9; WAM 80.783, locality 10; WAM 80.981, locality 12; WAM 81.2639, locality 15. One hundred and forty-two additional specimens, localities 1, 2, 4–13, 15–21, 23, 25, and 26.

Description. Shell large, the umbilical width ranging from 22 to 28 % of the shell diameter. Whorls nearly equidimensional to slightly depressed, whorl breadth/whorl height ratios ranging from 0·96 to 1·19, widest on the dorsal flanks. Umbilical wall vertical at is base but curving outward to pass smoothly into gently rounded umbilical shoulder. Flanks weakly convex, and slightly convergent; the venter is broadly arched. Broad primary ribs appear at a shell diameter of less than 10 mm and increase quickly in number to ten to twelve per whorl. They are very weak and rursiradiate on the umbilical wall, strengthen on the dorsal flanks where they are rectiradiate and form elongate bullae, and weaken on the mid-flank region. Broad secondary ribs, confined to the ventral flanks and venter, appear at a shell diameter of 45–55 mm. They are rectiradiate or weakly prorsiradiate, weaken noticeably on the mid-ventral line, and number thirty to thirty-six per whorl. Primary ribs pass into one or two secondaries in the mid-flank region but often with an offset junction suggesting that the two rib sets are slightly out of phase. At a shell diameter of about 145 mm, the primaries disappear and the secondaries become slightly weaker. The suture is typical of the genus; florid with L and I deeply incised and trifid, and U retracted on the umbilical wall.

Remarks. The largest specimen is a septate whorl fragment, showing weak secondary ribs at a whorl height of 10·5 cm, which corresponds to a shell diameter of some 25·5 cm. Shell dimensions (text-fig. 14) show no detectable ontogenetic change in whorl proportions but the relative umbilical diameter decreases slightly with growth. The spread in relative whorl breadth is in part an artefact, some measurements having been taken on the crests of bullae whereas others were taken between bullae. Umbilical tubercles vary in strength both on individual specimens and between specimens, being compact and strong at one extreme and elongate and weak at the other. In some specimens the secondary ribs are quite strong on the margins of the venter but disappear on the ventral midline so that they have the appearance of weak ventrolateral bullae. On others they are only slightly weakened on the ventral midline.

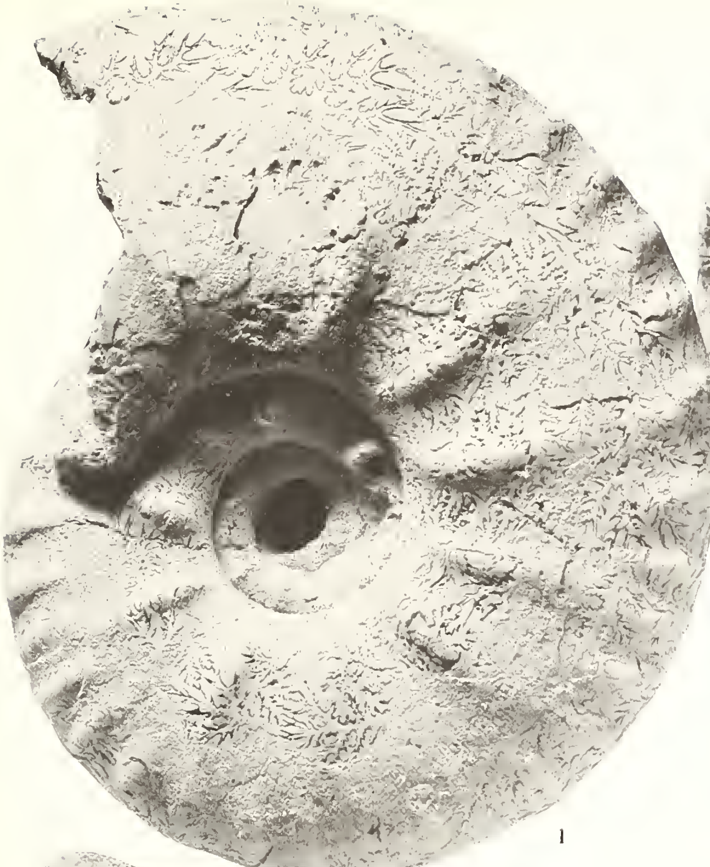
P. (*P.*) *jacquoti* is known from France (Seunes 1890, 1891) and has been described from British Columbia (Usher 1952), Armenia (Atabekian and Akopian 1969), and Madagascar (Collignon 1971). It has at times been confused with *P.* (*P.*) *neubergicus* (von Hauer) but the Western Australian collections show that the two species are quite separate. *P.* (*P.*) *neubergicus* is set apart by its more compressed whorl profile and more closely spaced secondary ribs. The specimen figured by de Grossouvre (1894, pl. 26, fig. 3*a*, *b*) and Collignon (1938, pl. 8, fig. 4, 4*a*, 4*b*) as *neubergicus* are better placed in *jacquoti*.

The type series of *P.* (*P.*) *jacquoti* (Seunes 1890, p. 5, pl. 2, figs. 1*a*, *b*, 3*a*, *b*) is indistinguishable from the Western Australian suite up to shell diameters of 8 cm. However, a difference is apparent in

EXPLANATION OF PLATE 8

Figs. 1–2, 7–10. *Pachydiscus* (*Pachydiscus*) *jacquoti australis* subsp. nov. 1–2, paratype, WAM 82.3082, × 1. 7–8, paratype, WAM 81.2431, × 1. 9–10, paratype, WAM 81.2639, × 1.

Figs. 3–6. *Pachydiscus* (*Pachydiscus*) *fresvillensis* Seunes. 3–4, NMV P31024, × 1. 5–6, WAM 60.761, × 1.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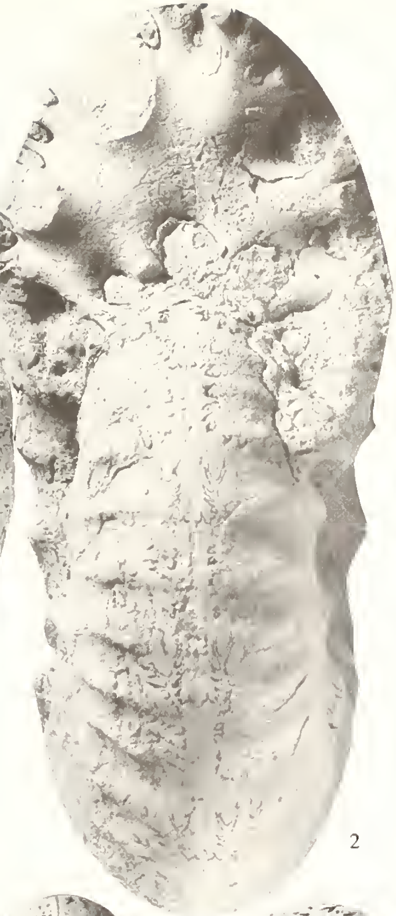
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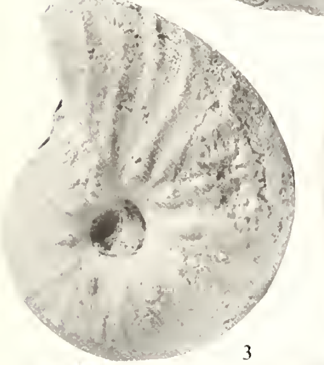
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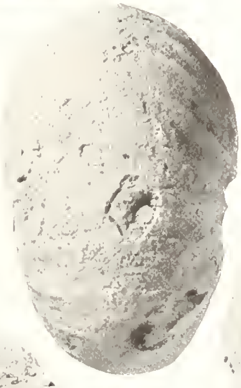
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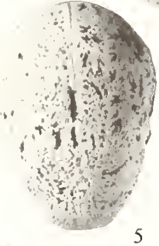
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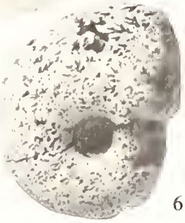
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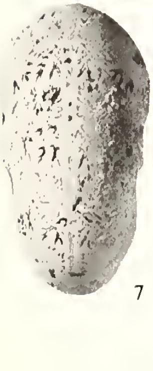
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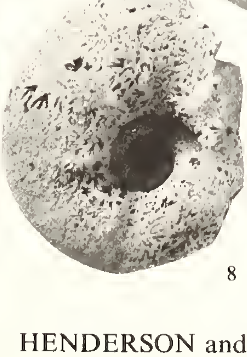
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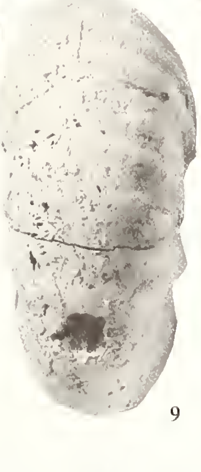
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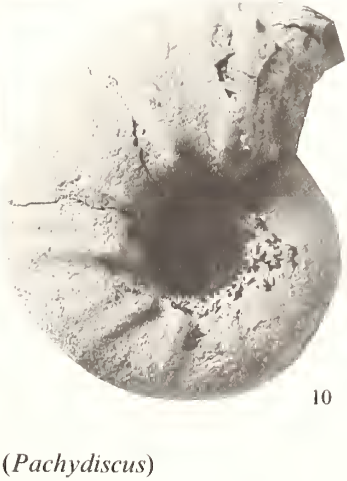
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HENDERSON and McNAMARA, *Pachydiscus* (*Pachydiscus*) mature ornamentation. Whereas the Western Australian specimens retain secondary ribs at all known stages of growth (text-fig. 14) up to a shell diameter of 25 cm, they disappear at a shell diameter of 8 cm on the French types. Accordingly the Western Australian suite is segregated as a subspecies. *P.* (*P.*) *egertoni* (Forbes 1846, p. 108, pl. *a*, fig. 1*a–c*) is a close ally of *P.* (*P.*) *jacquoti*, differing only in its more effaced ornament and the more distinctly convergent flanks of later whorls. Its juvenile growth stages, described by Forbes (1846, p. 103, pl. 7, fig. 8*a–c*) as *Ammonites ganesa*, also show effaced ribbing and have fewer umbilical bullae than those of *P.* (*P.*) *jacquoti*. The status of other Indian specimens figured by Stoliczka (1864, pl. 15, fig. 4*a–c*) and Kossmat (1898, p. 15, fig. 4*a–c*) as *P.* (*P.*) *egertoni* is uncertain. They are more strongly ornamented than Forbes's type series (BM C51038 and C51043) and may well represent *P.* (*P.*) *jacquoti*.

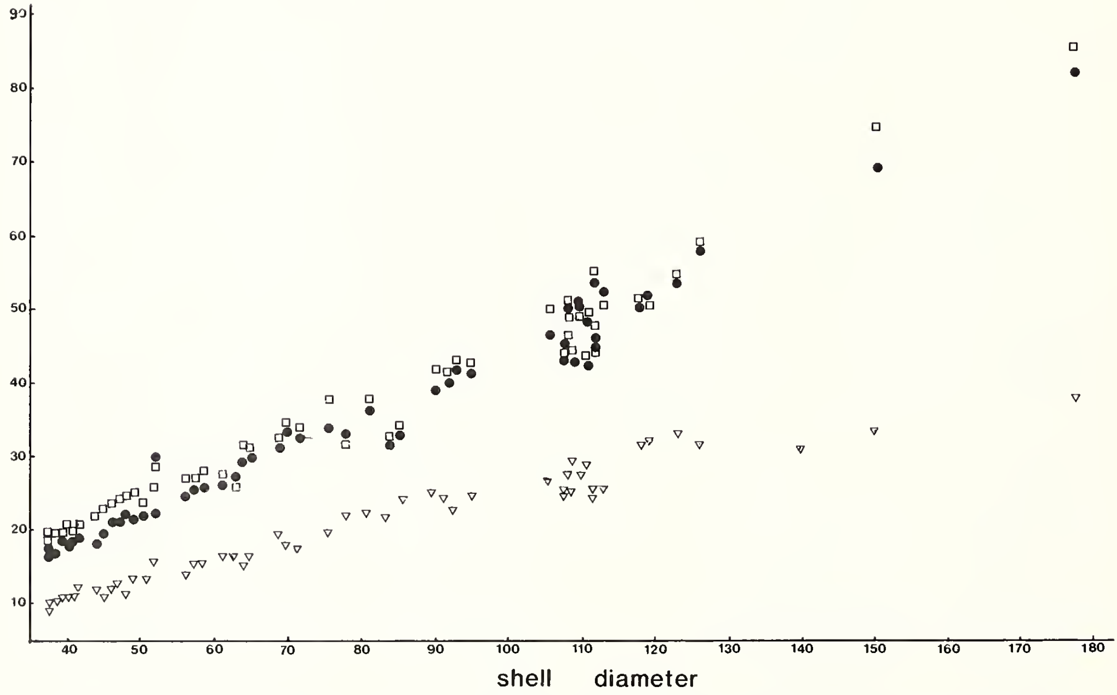
Other *Pachydiscus* species of similar morphology include *P.* (*P.*) *colligatus* (van Binkhorst, 1861), *P.* (*P.*) *epiplectus* (Redtenbacher, 1873), *P.* (*P.*) *fresvillensis* Seunes, 1890, and *P.* (*P.*) *subrotundus* Seunes, 1890. They are distinguishable from *P.* (*P.*) *jacquoti* by the nature of the ribs which all begin from the umbilical wall or dorsal flanks so that secondary ribs cannot be discriminated .

French *P.* (*P.*) *jacquoti* are of Maastrichtian age but the species also occurs in the Pender Formation, British Columbia (Usher 1952), which is of Campanian age (Ward 1978).

Pachydiscus (*Pachydiscus*) *fresvillenis* Seunes, 1890

Plate 8, figs. 3–6; Plate 9, figs. 1, 2; text-figs. 12*b*, 13*a*, 15*b*

1865 *Ammonites arrialoorensis* Stoliczka, p. 126 *pars*, pl. 63, fig. 2, 2*a* (*non* pl. 63, fig. 3, 3*a*; pl. 64, fig. 1, 1*a*).
1890 *Pachydiscus fresvillensis* Seunes, p. 3, pl. 1, fig. 1*a*, *b*.
1891 *Pachydiscus fresvillensis* Seunes; Seunes, p. 14, pl. 3, fig. 1*a*, *b*.



TEXT-FIG. 14. Shell dimensions of *Pachydiscus* (*Pachydiscus*) *jacquoti australis* subsp. nov. Squares represent whorl breadth, dots represent whorl height, and triangles represent umbilical diameter. Scales are in millimetres.

1906 *Pachydiscus supremus* Petho, p. 88, pl. 5, fig. 1*a*, *b*.
1908 *Pachydiscus colligatus* van Binkhorst; de Grossouvre, p. 28 *pars*, pl. 4, fig. 3*a*, *b*; pl. 5, fig. 1*a–c*; ?pl. 4, figs. 1*a*, *b*, 2; pl. 6, fig. 1*a–c*.
1938 *Parapachydiscus colligatus* van Binkhorst; Collignon, p. 30, pl. 5, fig. 1, 1*a*.
1938 *Parapachydiscus fresvillensis* Seunes; Collignon, p. 57, pl 7, figs. 4, 4*a*, *b*, 5.
1955*a* *Pachydiscus* sp. aff. *colligatus* van Binkhorst; Collignon, p. 74, pl. 26, fig. 2, 2*a*, 2*b*.
1969 *Pachydiscus colligatus fresvillensis* Seunes; Atabekian and Akopian, p. 13, pl. 6, fig. 1*a–b*.
1971 *Pachydiscus frevillensis* Seunes; Collignon, p. 30, pl. 652, fig. 2408.
1971 *Pachydiscus colligatus* van Binkhorst; Collignon, p. 31, pl. 653, pl. 654, fig. 2409.

Material. Thirty specimens, localities 4, 5, 7, 10–12, 15, 16, 18, 19, 23, and 26.

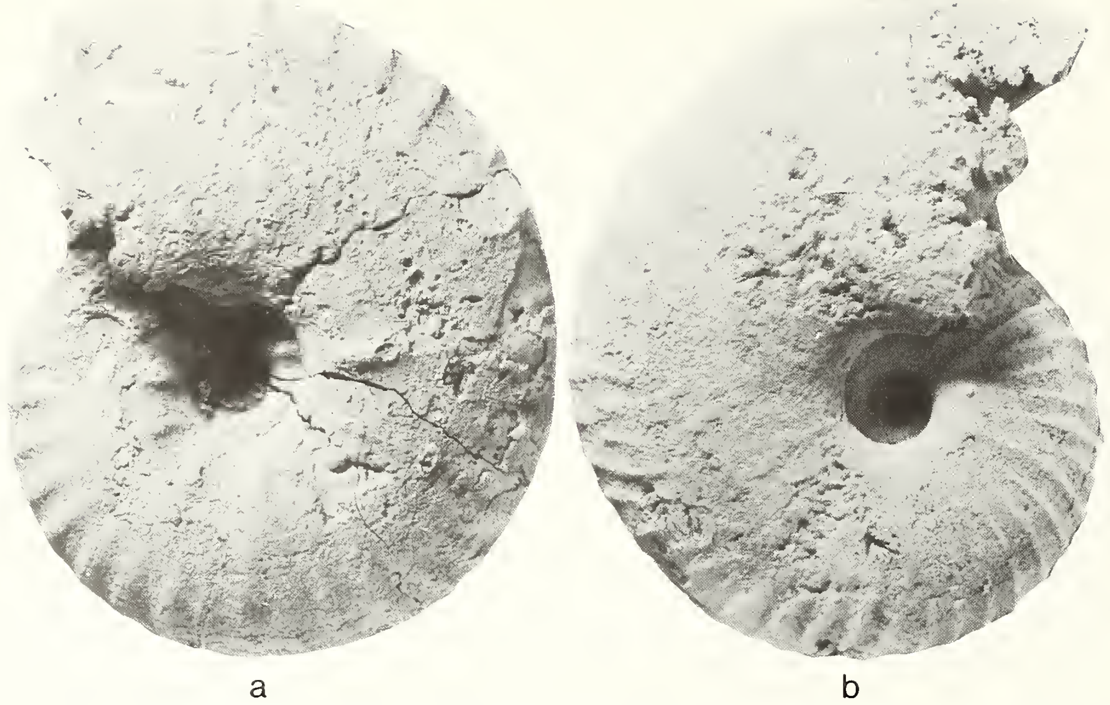
Description. Shell involute with the umbilicus measuring 15–21% of the shell diameter. Early whorls are depressed with strongly convex flanks and a broadly arched venter; the whorl breadth/whorl height ratio is about 1·4 at a shell diameter of 3 cm declining to about 1·2 at a shell diameter of 6 cm. At growth stages exceeding about 12·5 cm the whorl profile becomes compressed, the flanks gently convex and slightly convergent, and the venter more narrowly rounded. At its base, the umbilical wall is slightly overhanging. Maximum whorl breadth lies on the dorsal flanks for all stages of ontogeny. Early growth stages, up to a shell diameter of 6 cm, have nine to eleven umbilical bullae per whorl each giving rise to one or two ribs with an equal number of intercalatories beginning from the dorsal flanks so that there are some thirty ribs per whorl. At first they are thin and weak, especially across the venter, but they strengthen progressively with growth. Some can be followed as a faint rursiradiate trace on the umbilical wall; they are rectiradiate across the flanks but curve forward at the margin of the venter across which they are gently projected. Later growth stages, at shell diameters of 60–120 mm, have eight to nine umbilical bullae each giving rise to one to two ribs with one to three intercalatories beginning from the dorsal flanks to make thirty-seven to forty-two ribs per whorl. Ribs are equally strong on the flanks and venter and correspond in shape to those of earlier volutions. At a shell diameter of about 120 mm, umbilical bullae disappear and ribs become confined to the ventral flanks and venter. Suture typical of the genus except that the umbilical lobe is only slightly retracted on the umbilical shoulder and wall.

Dimensions.

	D	H	B	B/H	U	%
WAM 60.761	32·0	15·8	21·8	1·38	5·2	16
NMV P31024	49·5	24·5	30·5	1·24	8·5	17
WAM 81.2388	56·2	26·2	33·5	1·28	11·8	21
WAM 81.2528b	63·0	31·0	36·8	1·19	13·5	21
WAM 81.2707	105·0	53·0	55·5	1·05	19·0	18
WAM 81.2527	123·0	62·0	62·0	1·00	23·5	19
OUM KZ13678	138·0	67·0	69·0	1·02	28·0	20
WAM 81.2623	154·0	80·5	76·0	0·94	25·0	16
NMV P31014	181·0	93·0	84·0	0·90	28·0	15

Remarks. The larger Western Australian specimens are inseparable from the holotype of *P.* (*P.*) *fresvillensis* Seunes (1890, pl. 1, fig. 1*a*, *b*) with which they have been compared by means of a cast (OUM KZ13678) held by the University Museum, Oxford. Ornament of the holotype matches exactly, with the dorsal flanks becoming smooth at a shell diameter of about 12 cm. Its juvenile growth stages are not shown but the whorl profile is depressed (whorl breadth/whorl height ratio of 1·18) at the earliest stage at which it can be measured, corresponding to a shell diameter of some 75 mm.

The identity of *P.* (*P.*) *fresvillensis* is much confused in the literature; its relationship to *P.* (*P.*) *colligatus* (van Binkhorst, 1861) in particular has been held in question. The type series of *P.* (*P.*) *colligatus* (van Binkhorst 1861, pls. 7, 8, 8*a*) consisted of two complete specimens, measuring nearly 290 mm and 45 mm in diameter, and a number of whorl fragments. Both the complete specimens have effaced ornament with umbilical tubercles lacking and, in common with the fragmentary specimens, an equidimensional whorl profile. Some of the whorl fragments, however, are quite strongly ribbed and possess umbilical tubercles. It may well be that the type series includes more than one species. The interpretation of *P. colligatus* adopted here is based on the two complete specimens which are distinguished from *P.* (*P.*) *fresvillensis* by their effaced ribbing, especially that of the



TEXT-FIG. 15. Mature growth stages of *Pachydiscus* species, ×0·5. *a*, *P.* (*P.*) *jacquoti australis* subsp. nov., holotype, WAM 80.1004. *b*, *P.* (*P.*) *fresvillensis* Seunes, NMV P31014.

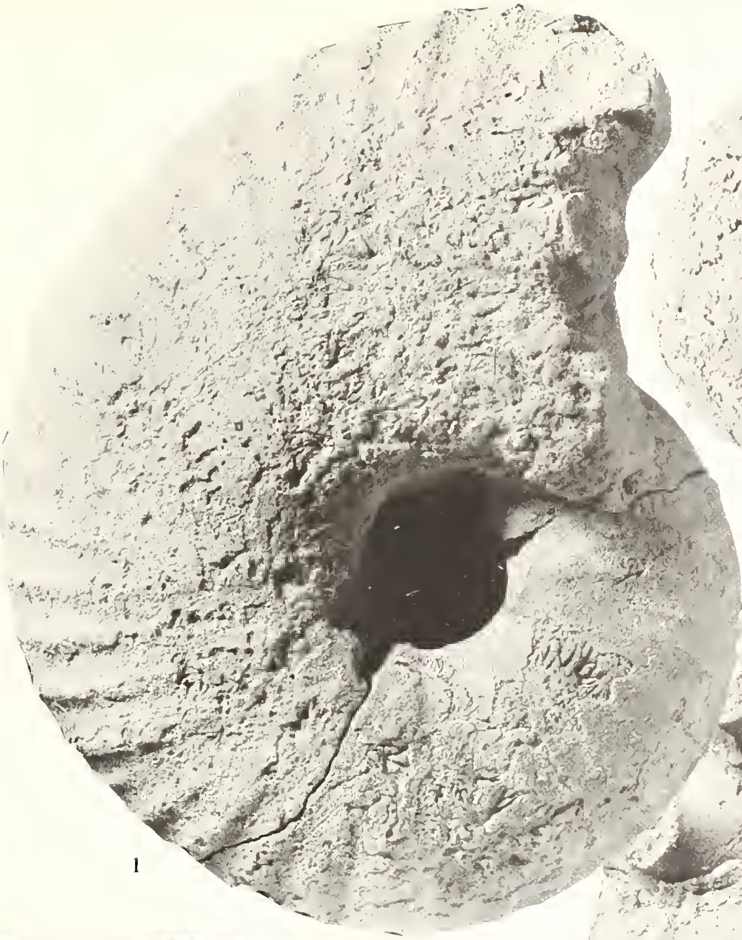
mature volutions, and by the equidimensional rather than strongly depressed whorl profile of the initial growth stages.

P. colligatus is here regarded as a senior synonym of *P. ootacodensis* (Stoliczka), 1865, a species which has also remained poorly defined in spite of revision by Kossmat (1898) who segregated one of Stoliczka's type series, a large specimen with distinctive, strong ornament, as *P. grossouvrei* Kossmat. Stoliczka (1865, p. 110) also recognized these species as synonymous but regarded *A. colligatus* van Binkhorst, 1861 as a primary homonym of *A. colligatus* Hoeninghaus, 1830 whereby *ootacodensis* became the valid name. However, *A. colligatus* Hoeninghaus was published merely as part of a list and is a *nomen nudum*, without nomenclatural status. *P. ootacodensis* has been well documented from the Pacific coast of North America by Whiteaves (1895), Usher (1952), and Jones (1963). The North American suite includes specimens with very effaced ornament as well as some, especially juveniles, with stronger ribbing and incipient umbilical tubercles. Jones (1963) segregated the latter as a new species, *P.* (*P.*) *hornbyense*, but the suite shows continuous variation and is best regarded as comprising a single, somewhat variable species. As noted by Matsumoto (1959*b*), the Californian species *P.* (*P.*) *stanislausensis* Anderson, 1958 is probably also a synonym of *P.* (*P.*) *colligatus*

EXPLANATION OF PLATE 9

Figs. 1–2. *Pachydiscus* (*Pachydiscus*) *fresvillensis* Seunes, WAM 81.2527, ×1.

Figs. 3–6. *P.* (*P.*) *neubergicus dissitus* subsp. nov. 3–4, paratype WAM 80.963, ×1. 5–6, paratype WAM 60.54, ×1.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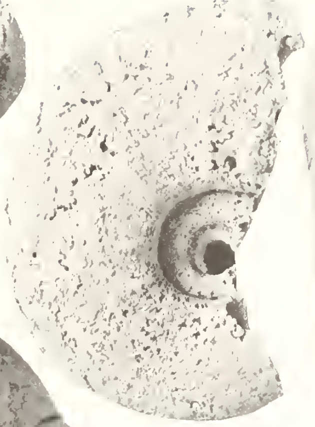
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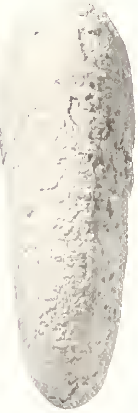
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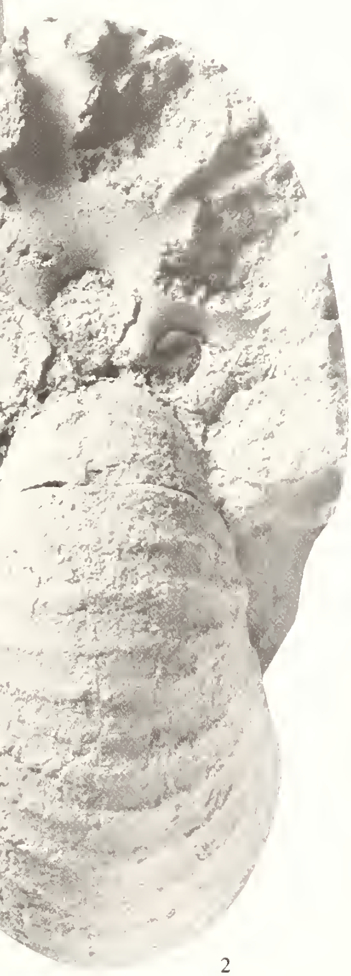
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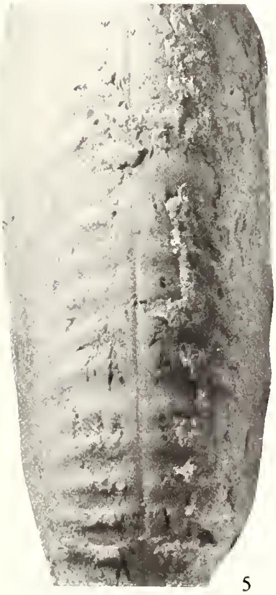
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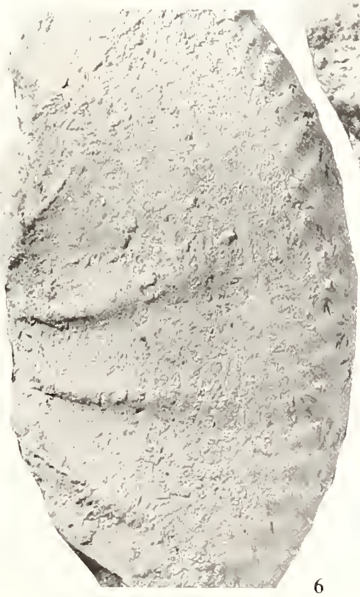
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HENDERSON and McNAMARA, *Pachydiscus* (*Pachydiscus*)

(= *P. ootacodensis*). All specimens of this assemblage are readily distinguished from *P.* (*P.*) *fresvillensis* by virtue of effaced ornament and the juvenile growth stages which are not depressed. The large specimen with strong, mature ribbing figured by Stoliczka (1865, pl. 56, fig. 1) appears to be an exception but the figure is composite, the ribs having been taken from another, and otherwise unfigured, specimen whose specific identity is questionable.

P. (*P.*) *colligatus* and its synonyms and *P.* (*P.*) *fresvillensis* have commonly been confused with two other species, *P.* (*P.*) *epiplectus* Redtenbacher, 1873 and *P.* (*P.*) *subrobustus* Seunes, 1890. Both of these taxa have ornament of comparable style and strength to that of *P.* (*P.*) *fresvillensis* but their initial volutions differ in not being strongly depressed. In addition, the pre-adult ribbing of *P.* (*P.*) *epiplectus* is more closely spaced (some twenty-eight per half whorl). De Grossouvre (1894) regarded *colligatus*, *epiplectus*, and *fresvillensis* as synonyms. In the interpretation preferred here, one of his figured specimens (pl. 24, figs. 1, 3) probably represents *P.* (*P.*) *subrobustus* whereas the other (pl. 33, figs. 1, 2) represents *P.* (*P.*) *epiplectus*. Armenian specimens figured by Mikhailov (1951, pl. 5, fig. 28; pl. 6, fig. 33) as *P.* (*P.*) *colligatus* and *P.* (*P.*) *colligatus* var. *epiplectus* respectively are here regarded as *P.* (*P.*) *epiplectus*. *P.* (*P.*) *haueri* Collignon (1955*a*, p. 75), established for *P.* (*P.*) *neubergicus* von Hauer *pars* (1858, pl. 3, figs. 1, 2), is allied to *P.* (*P.*) *neubergicus* but distinguished by its ribs which are not projected on the venter. The Armenian specimen figured by Atabekian and Akopian (1969, pl. 8, fig. 1) as *P. haueri haueri* is in fact *P.* (*P.*) *epiplectus*. *P.* (*P.*) *colligatus* (*s.s.*) and *P. colligatus michailovi* of Atabekian and Akopian (1969), like *P. colligatus latiumbilicatus* of Błaszkiewicz (1980), are too strongly ribbed for reference to that species and better considered as *P. subrobustus* Seunes.

Part of the suite figured by de Grossouvre (1908) as *P. colligatus*, certainly the originals of his pl. 4, fig. 2*a*, *b* and pl. 5, fig. 1*a–c*, show the distinctive depressed initial volutions and are typical *P. fresvillensis*. The small specimen illustrated by Stoliczka (1865, pl. 63, fig. 2, 2*a*) as *P. arrialoorensis* (Stoliczka) is unrelated to the remainder of the type series of that species but indistinguishable from Western Australian *P. fresvillensis* of the same size. *P. supremus* Petho, 1906 also joins the synonymy; it is based on a large Yugoslavian specimen which is very like the largest of the Western Australian suite. All the Madagascan specimens referred by Collignon (1938, 1955*a*, 1971) to *P. colligatus* are quite strongly ribbed and appear to possess depressed early volutions. They are also grouped in *P. fresvillensis*. The Chilean *P. quiriquinae* Steinmann, 1895, known only from a single, very large specimen, may perhaps represent *P. fresvillensis* but appears to be distinct by virtue of its very weak mature ornament.

The distribution of *P. fresvillensis* embraces eastern and western Europe, Madagascar, southern India, and Western Australia and its established range is late Campanian (*Bostrychoceras polyplocum* Zone) to Maastrichtian.

AGE OF THE MIRIA FORMATION

In order to assign an age to the Miria Formation on the basis of its ammonite fauna, it is necessary to review current knowledge of ammonites from the type Maastrichtian and correlative sequences in northern Europe.

Ammonites from the type Maastrichtian of Limburg are poorly known. The classic descriptions of van Binkhorst (1861) and de Grossouvre (1908) were based on small collections of generally poor preservation which have not subsequently been revised. The assemblage they described comprises: *Anagaudryceras* sp., *Sphenodiscus binckhorsti* Bohm, *Pachydiscus* (*Pachydiscus*) *colligatus* (van Binkhorst), *P.* (*P.*) *fresvillensis* Seunes, *P.* (*P.*) *gollevillensis* (d'Orbigny), *Baculites* spp., *Eubaculites* sp., *Hoploscaphites constrictus* (Sowerby), *Diplomoceras cylindraceum* (Defrance), and *Glyptoxoceras* sp. Of these, *S. binckhorsti* is known to occur in the highest member of the Maastricht Formation, the Meersen Chalk (Felder *et al.* 1980), whereas several of the other taxa, including de Grossouvre's (1908) *P.* (*P.*) *neubergicus* (von Hauer), were recorded from the older Kunraed Limestone. A twofold ammonite zonation of the standard Maastrichtian Stage with an upper zone of *Sphenodiscus* sp. and a lower zone of *P.* (*P.*) *neubergicus*, presumably based on these data, has been adopted by many workers (Spath 1926; Arkell, Kummel and Wright 1957; Kennedy and Cobban 1976; Wiedmann 1979). However, no detailed biostratigraphic data for ammonites in the type Maastrichtian is available. Furthermore, de Grossouvre's (1908) record of *P.* (*P.*) *neubergicus* is erroneous. The specimens he referred to this species display a nearly equidimensional whorl profile and probably represent *P.* (*P.*) *jacquoti*.

A fourfold belemnite zonation, widely represented throughout northern Europe, has allowed the recognition of the Maastrichtian Stage in several other sequences for which data on the ranges of ammonites are now available. Birkelund (1979) summarized the range data for ammonites in the white chalk of Denmark and later (Birkelund 1982) detailed the biostratigraphy of ammonites in a Maastrichtian chalk quarry at Hemmoor, north-western Germany. The most comprehensive, controlled biostratigraphic zonation is that of Blaszkiewicz (1980), based on the sequence and faunas of the middle Vistula River valley, Poland.

Other general descriptions of Maastrichtian ammonite faunas which make no contribution to a detailed zonation are available for France (d'Orbigny 1840–1842; Seunes 1890–1891; de Grossouvre 1894; see Sornay 1959) and Germany–Austria (Schlüter 1871–1876; Redtenbacher 1873; Thiedig and Wiedmann 1976; see Wiedmann 1979).

A number of conclusions may be reached concerning current knowledge of Maastrichtian ammonite faunas and biostratigraphy in north-western Europe:

1. The assemblage contains a number of distinctive species whose ranges appear to be restricted to the Maastrichtian. In addition to those listed above for the type sequence, these include *Phylloceras* (*Neophylloceras*), *Desmophyllites*, *Saghalinites wrighti* Birkelund, authentic *Pachydiscus* (*P.*) *neubergicus* (von Hauer), *P.* (*P.*) *jacquoti* Seunes, *Pseudokossmaticeras tercense* (Seunes), *Brahmaites* (*Anabrahmaites*) *haugi* (Seunes), *H. tenuistriatus* (Kner), *Acanthoscaphites varians* (Lopuski), *Neancyloceras*, *Nostoceras*, and perhaps *Phylloptychoceras*.
2. Of the genera, only *Sphenodiscus*, *Brahmaites* (*Anabrahmaites*), and *Eubaculites* are not known to range into the Campanian. *Diplomoceras* may also be a restricted Maastrichtian element but the lower limit of its range is open to question.
3. As noted by Birkelund (1982), marked discrepancies occur between species ranges in those sequences for which biostratigraphic detail is known, precluding the recognition of useful zones within the Maastrichtian until a larger body of data is available.
4. Most of the species are endemic to northern Europe, except for those of *Pachydiscus* (*Pachydiscus*) which are widely distributed. The latter, together with the genera *Eubaculites*, *Sphenodiscus*, and *Brahmaites*, offer the best prospects of correlating other Maastrichtian sequences with those of northern Europe.

Direct correlation of the ammonite fauna from the Miria Formation with that of Maastrichtian age in northern Europe is afforded by the shared species of *Pachydiscus* (*Pachydiscus*), *P.* (*P.*) *neubergicus*, *jacquoti*, and *fresvillensis*. Heteromorphs from the Miria Formation we will fully revise elsewhere. We list *Baculites*, *Eubaculites*, *Glyptoxoceras*, and *Diplomoceras* and regard all the new genera proposed by Brunnschweiler (1966) as synonyms. *Nostoceras*, recorded by Brunnschweiler (1966) as from the Miria Formation, we believe to be from the uppermost interval of the underlying Korojon Calcarenite. All four heteromorph genera are also represented in the Maastrichtian fauna of northern Europe. Other shared elements, *Phylloceras* (*Neophylloceras*), *Anagaudryceras*, and *Desmophyllites*, are all long-ranging forms.

The fauna of the Miria Formation is closely allied to that of the Maastrichtian Valudayur zone of Pondicherry, southern India, described by Forbes (1846), Stoliczka (1863–1866), and Kossmat (1895, 1897*a*, 1898) and provided with a biostratigraphic framework by Kossmat (1897*b*). All the Miria Formation genera, with the exception of the kossmaticeratids other than *Brahmaites*, are shared as are the species. *P.* (*N.*) *surya* (Forbes), *Partschiceras* (*Phyllopachyceras*) *forbesianum* (d'Orbigny), *Gaudryceras kayei* (Forbes), *Pseudophyllites indra* (Forbes), *D. diphylloides* (Forbes), *Pachydiscus* (*P.*) *neubergicus* (von Hauer (= A. chrishna Forbes) and *E.* cf. *vagina* (Forbes). The assemblage from that horizon of the Ariyalur Stage, Trichinopoly, southern India, which crops out at Ootacod and contains *A. subtilineatum* (Kossmat), *Gunnarites kalika* Stoliczka), *Brahmaites* (*Brahmaites*) cf. *kossmati* sp. nov. and *Eubaculites* (see Stoliczka, op. cit., Kossmat op. cit.) is also correlative with the Miria Formation, as are the faunas from Madagascar (see Besairie 1972) and south-eastern Africa (see Kennedy and Klinger 1975) which have been assigned a Maastrichtian age.

The Maastrichtian age assigned to the ammonites herein is wholly in agreement with data from Foraminifera. Edgell (1957) assigned a Maastrichtian age to the Miria Formation on the basis of contained *Globotruncana contusa* (Cushman). He recognized the Campanian–Maastrichtian boundary within the underlying Korojon Calcerenite, the upper part of which contains benthic Foraminifera typical of the Maastrichtian while the lower part has *G. arca* (Cushman) and other typical Campanian elements. Investigations by Belford (1958) into foraminiferal biostratigraphy of the Miria Formation and underlying units realized the same conclusion. Brunnschweiler (1966) rejected the age assignments of these workers. He considered the kossmaticeratid taxa, with the exception of *Brahmaites*, to be restricted to the lower part of the Miria Marl and to indicate a late Campanian age whereas the upper part of the formation contained a different assemblage and is of Maastrichtian age.

Our investigations do not support Brunnschweiler's view. Most of the ammonites from the Miria Formation are from float and *in situ* specimens are uncommon. To evaluate the possibility of an age difference between various elements of the assemblage, matrix samples from specimens of *Pseudophyllites indra*, *D. diphylloides*, *Gunnarites kalika*, *Maorites densicostatus*, *Pachydiscus* (*P.*) *jacquoti australis* and *P.* (*P.*) *fresvillensis* were processed for Foraminifera. Determinations by Dr. M. B. Hart (pers. comm.) have shown that all the samples contain a Maastrichtian assemblage typified by *Globotruncana gansseri* (*s.l.*), *G. contusa*, *G. arca*, and *Rugoglobigerina rugosa*.

In addition, we have examined sections of the Miria Formation exposed at localities 15–17, 19–21, and 23–25. All sections display the same sequence: an upper portion (0·5–0·75 m) with abundant ammonites and a lower portion (1–2 m) in which ammonites are uncommon to rare. The kossmaticeratids *Gunnarites kalika*, *G. raggatti*, *M. densicostatus*, *Grossouvrites gemmatus*, *Kossmaticeras* (*Natalites*) *brunnschwieleri* and *K.* (*N.*) sp. all occur in the upper portion. The few taxa we have determined from the lower portion, *Phylloceras* (*Neophylloceras*) *surya*, *Gaudryceras kayei*, *Pseudophyllites indra*, *Pachydiscus* (*P.*) *jacquoti australis*, and *Gunnarites kalika*, all have ranges extending into the upper portion.

Nor are there significant differences between collections from different localities of the Miria Formation as suggested by Spath (1941), even though collections have been made at intervals over a strike length of some 80 km.

Kossmaticeratids comprise more than a third of the Miria Formation's non-heteromorph ammonite assemblage and include representatives of *Gunnarites*, *Maorites*, *Kossmaticeras* (*Natalites*), *Neograhamites*, and *Grossouvrites* which have all previously been assigned a Campanian age. It is now apparent that marked late Cretaceous biogeographic provincialism (see Henderson 1970), rather than a temporal pattern, is responsible for the dominance of kossmaticeratid taxa in late Cretaceous ammonite assemblages from New Zealand, Patagonia, and the Antarctic Peninsula.

It may be that the ranges of *Neograhamites*, *G. gemmatus* (Huppé), and *M. densicostatus* (Kilian and Reboul) are restricted to the Maastrichtian. Part or all of the Snow Hill Island Series of the Antarctic Peninsula which contains these taxa may be of Maastrichtian age. Other elements shared by the Snow Hill Island Series with the Maastrichtian Valudayur zone of Pondicherry, India, and the Miria Formation, such as *Kitchinites*, *Pachydiscus* (*Pachydiscus*) closely allied to *gollevillensis*, *Diplomoceras*, and *Polyptychoceras* lend support to such a view.

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MICROFOSSIL DISTRIBUTION ACROSS THE BASE OF THE WENLOCK SERIES IN THE TYPE AREA

by J. E. MABILLARD *and* R. J. ALDRIDGE

ABSTRACT. Rich microfossil assemblages have been recovered from closely spaced samples collected from the uppermost Llandovery and lowermost Wenlock strata of the Wenlock Edge area. Large numbers of acritarchs, chitinozoans, conodonts, foraminiferans, ostracods, and other microfossils occur through the sampled sequence and provide a much better basis for correlation of the base of the Wenlock Series than can currently be achieved with macrofossil groups. The boundary cannot be shown to be coincident with the base of any biozone, but lies within the *amorphognathoides* conodont interval, between the base of acritarch zone 5 and the last occurrence of *Pterospathodus amorphognathoides*. At the stratotype locality for the base of the Wenlock Series, these horizons are separated by about 40 cm of strata. Elsewhere, the range of *P. amorphognathoides* encompasses much greater thicknesses of strata and, even using several fossil groups, the position of the boundary can only be broadly delimited.

IN 1971 the Stratigraphy Committee of the Geological Society of London established a working group to review the classification of the Wenlock Series of the Silurian System in the type area around Wenlock Edge, Shropshire. The results of this study (Bassett *et al.* 1975) included sections on lithostratigraphy, biostratigraphy, and chronostratigraphy. The revised chronostratigraphy, with the Wenlock Series divided into Sheinwoodian and Homerian Stages, was subsequently accepted by the Subcommission on Silurian Stratigraphy of the IUGS and the area is now ratified as the international type for the series (Holland 1980*a*, *b*). The base of the Wenlock Series was defined by Bassett *et al.* (1975, p. 13) at a standard section in Hughley Brook (NGR SO5688 9839), 200 m south-east of Leasows Farm (text-fig. 1).

In their consideration of the biostratigraphy of the Wenlock Series in the type area Bassett *et al.* (1975) concentrated on the graptolites, treating brachiopods and other macrofossils more briefly. They were able to establish the presence of graptolites through the succession, representing an almost complete zonal sequence from the late Llandovery *crenulata* Biozone to the late Wenlock *ludensis* Biozone. Although no graptolites were recorded from strata between 10 m below and 3·0–4·5 m above the Llandovery–Wenlock boundary, it has been assumed that the base of the *centrifugus* Biozone coincides with the base of the Wenlock Series (Holland 1980*a*).

Although microfossils were not considered in detail by Bassett *et al.* (1975), they noted the potential of several groups for correlation of the Wenlock Series and for recognition of the Llandovery-Wenlock boundary. Our sampling of the boundary beds has revealed extremely rich microfossil assemblages, and the purpose of this paper is to complement the data on macrofossils with detailed records of microfossil distribution in the uppermost Purple Shales and lowermost Buildwas Formation of the Wenlock type area. Our material is from two sections (text-fig. 1), the boundary stratotype near Leasows Farm and a parallel section in Harley Brook, near 'Domas' (NGR SJ5958 0077). These localities are numbers 25 and 24 of the Micropalaeontology Unit, Department of Geology, University of Nottingham.

At both localities, the lower Wenlock Buildwas Formation is conformable on the upper Llandovery Purple Shales. The boundary is not sharp, with a gradual lithological change apparent from the predominantly maroon mudstones and limestones of the Purple Shales to the calcareous, olive-grey, silty shales of the Buildwas Formation. At the Leasows section, the maroon colouration

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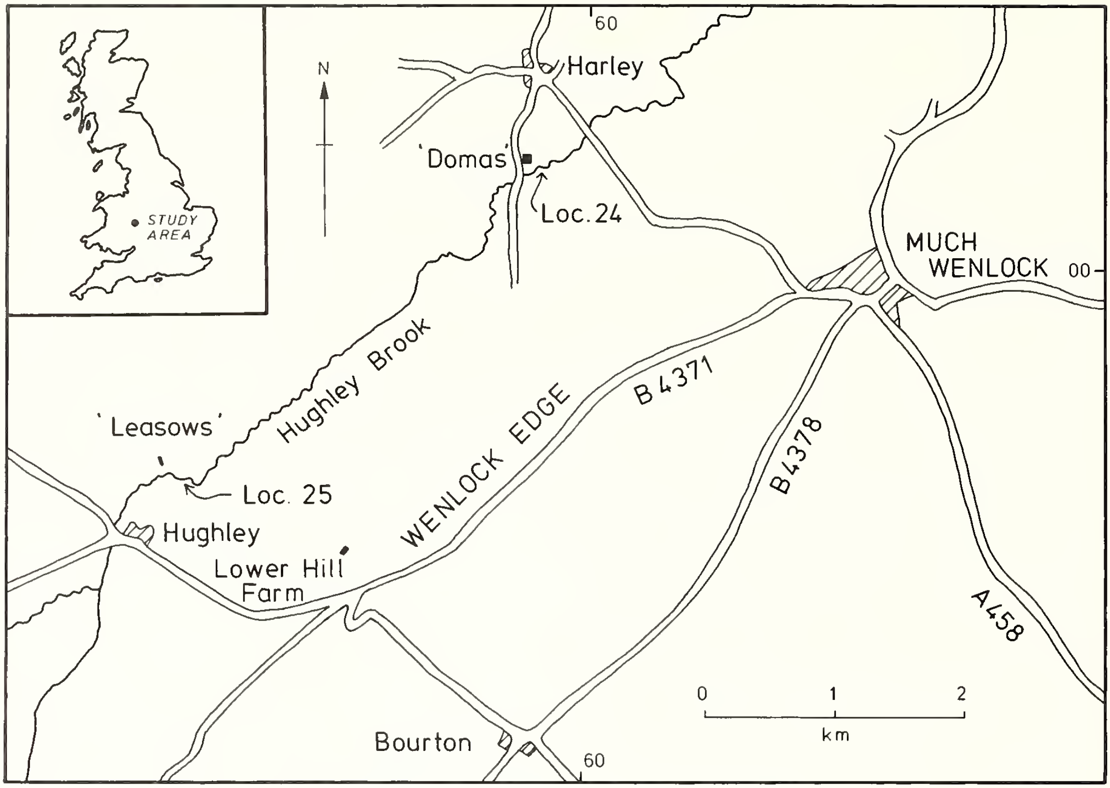


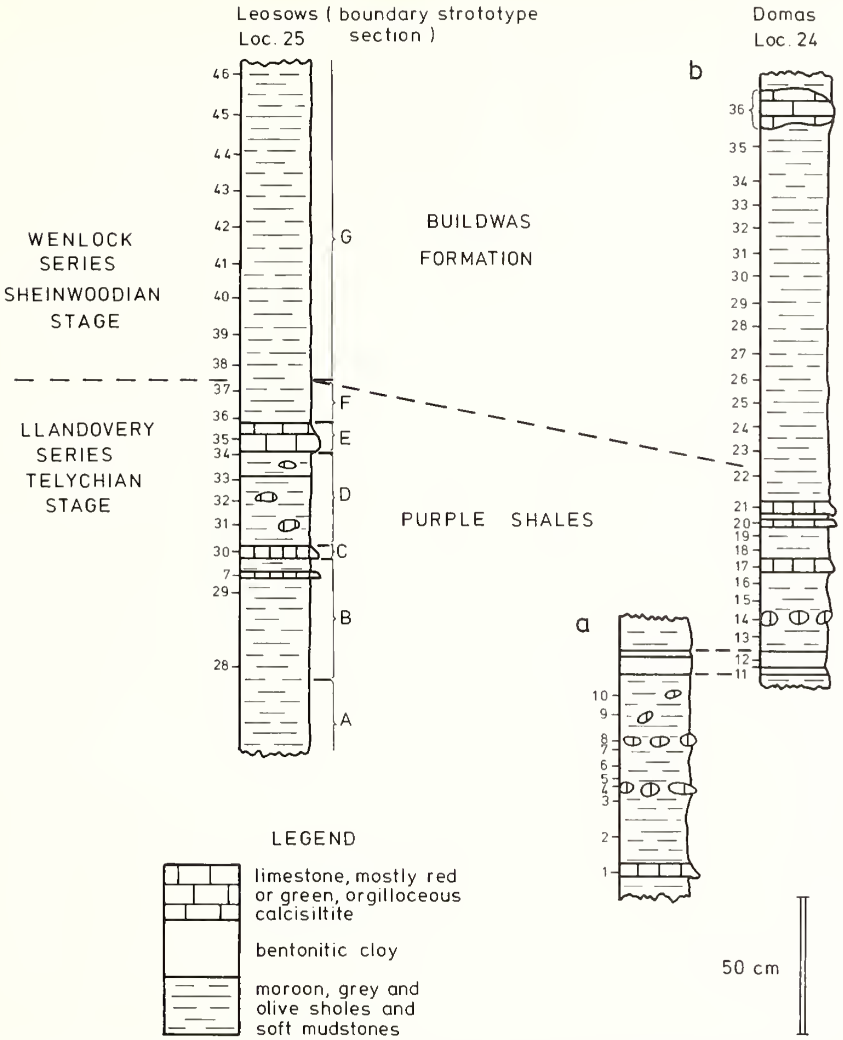
TEXT-FIG. 1. Localities of the sampled sections.

terminates fairly abruptly some 20 cm below the base of the Buildwas Formation, which, by definition, is also the base of the Wenlock Series. Macrofossils, particularly brachiopods, are common through the exposed sequence. The benthic macrofauna of the Purple Shales in the Wenlock Edge area is referable to the *Clorinda* or mixed *Clorinda-Costistricklandia* Community (Ziegler, Cocks and McKerrow 1968), and that of the Buildwas Formation to the *Dicoelosia biloba* Community (Hurst, Hancock and McKerrow 1978). Both formations appear to have been deposited in an open-marine, offshore shelf environment.

METHODS OF STUDY

Following reconnaissance sampling, a total of fifty-six samples was carefully collected 'bed-by-bed' from the two localities, with all lithologies represented (text-fig. 2). The mean sampling interval was less than 10 cm, and at each sampled horizon the smallest practicable thickness of sediment was removed.

Large numbers of microfossils were recovered from all samples except the probable bentonitic clay at 'Domas' (Sample 24/12). The standard sample weight processed for larger microfossils was 1 kg, except for samples 25/42–46, which weighed 500 gm. Shales were disaggregated using petroleum spirit followed by hot water, and limestones were digested with 10% acetic acid; all residues were washed through a 75 μm sieve. 'Heavy' and 'light' fractions of each residue were separated using bromoform; the heavy fraction, in which conodonts were concentrated, was picked completely, while a representative split of the larger light fraction was picked for other microfossils. Palynomorphs


Leasows (boundary stratotype section)
Loc. 25
Domas
Loc. 24
b
a
WENLOCK
SERIES
SHEINWOODIAN
STAGE
LLANDOVERY
SERIES
TELYCHIAN
STAGE
BUILDWAS
FORMATION
PURPLE SHALES
G
F
E
D
C
B
A
46
45
44
43
42
41
40
39
38
37
36
35
34
33
32
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19
18
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16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
LEGEND
limestone, mostly red or green, argillaceous calcisiltite
bentonitic clay
maroon, grey and olive shales and soft mudstones
50 cm

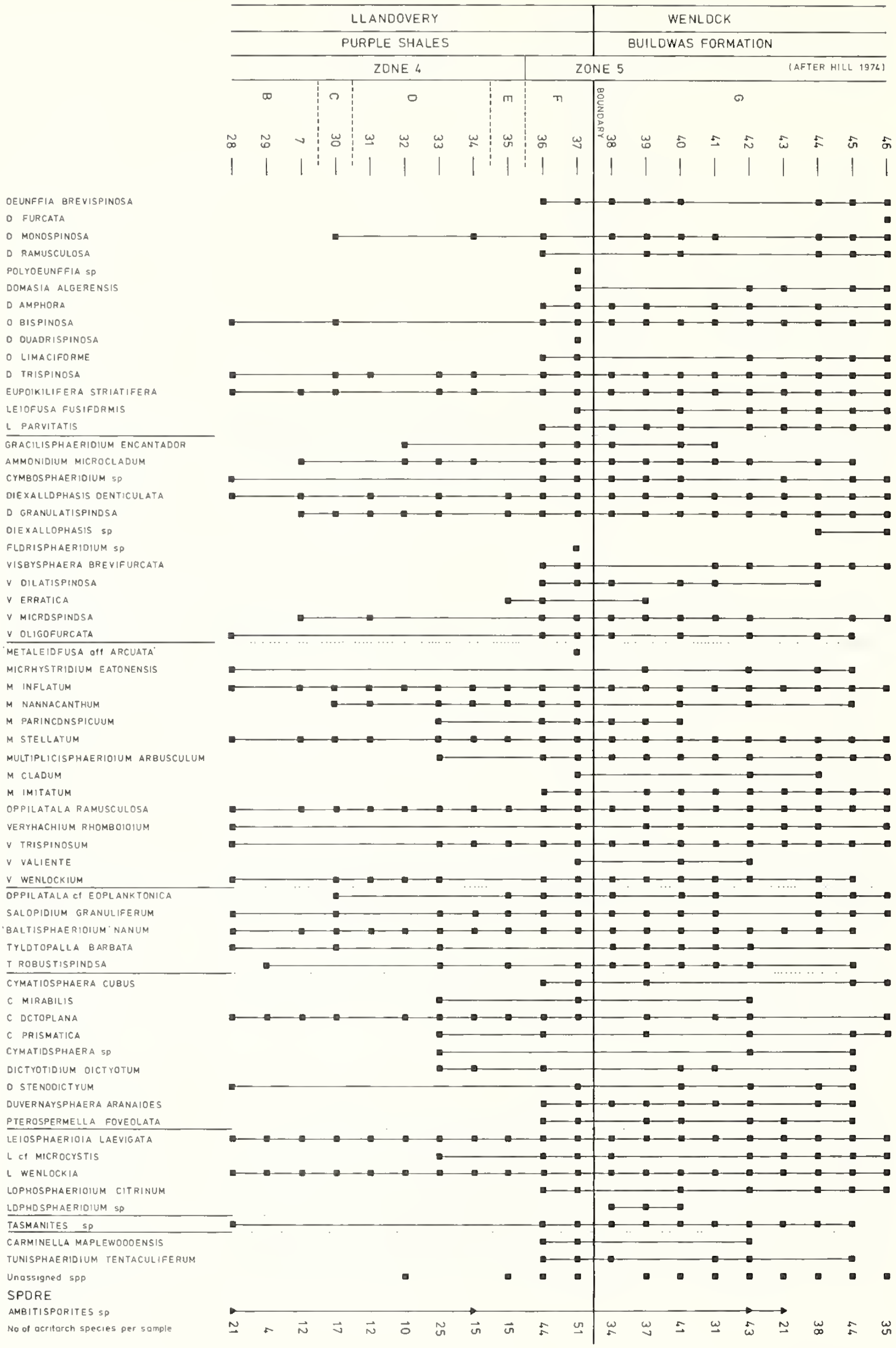
TEXT-FIG. 2. Measured sections at the two localities, showing sampled horizons. Units A–G at Leasows after Bassett *et al.* (1975, p. 13).

were extracted by preparation methods similar to those described by Neves and Dale (1963) and Sarjeant (1974).

MICROFOSSIL DISTRIBUTION

Acritarchs

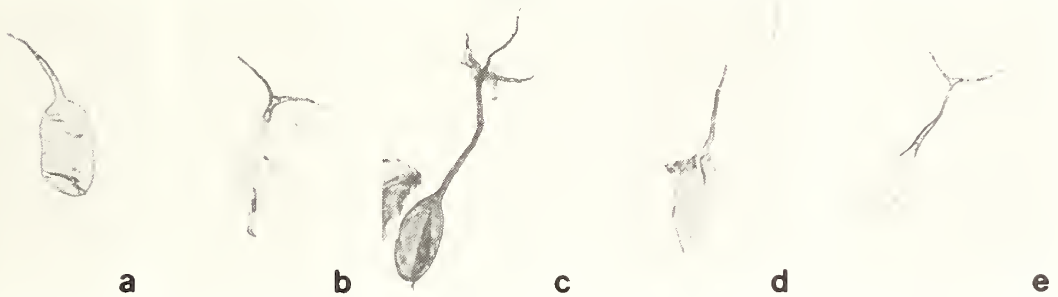
All palynological preparations from Leasows and Domas contain acritarchs (text-figs. 3, 4) which always form the greatest part of the assemblage. Chitinozoans, scolecodonts, melanosclerites, spores, organic linings of foraminiferal tests, fragments of graptolite theca, and structureless organic matter also occur in varying proportions. The preservation of acritarchs is good to excellent with body colour pale green to yellow, or brown in thicker-walled forms, which indicates a low thermal maturity. As most preparations contain many thousands of specimens no attempt was made to



TEXT-FIG. 3. Acritarch assemblages from the stratotype section for the base of the Wenlock Series at Leasows. For taxonomic comments and the authorship of most species see Dorning (1981*a*) and Aldridge *et al.* (1979).

determine absolute abundance. The relative proportions of species in preparations from the Purple Shales and Buildwas Formation have been documented by Hill (1974).

At Leasows, acritarchs are uncommon in the greater part of the Purple Shales (units B–E), particularly in the limestones. Assemblages from these lower, maroon-coloured units are dominated by thick walled sphaeromorphs such as *Leiosphaeridia wenlockia* Downie. In the uppermost Purple Shales (unit F) there is a significant increase in abundance and diversity which coincides with the lithological change to beds transitional to those of the overlying Buildwas Formation.



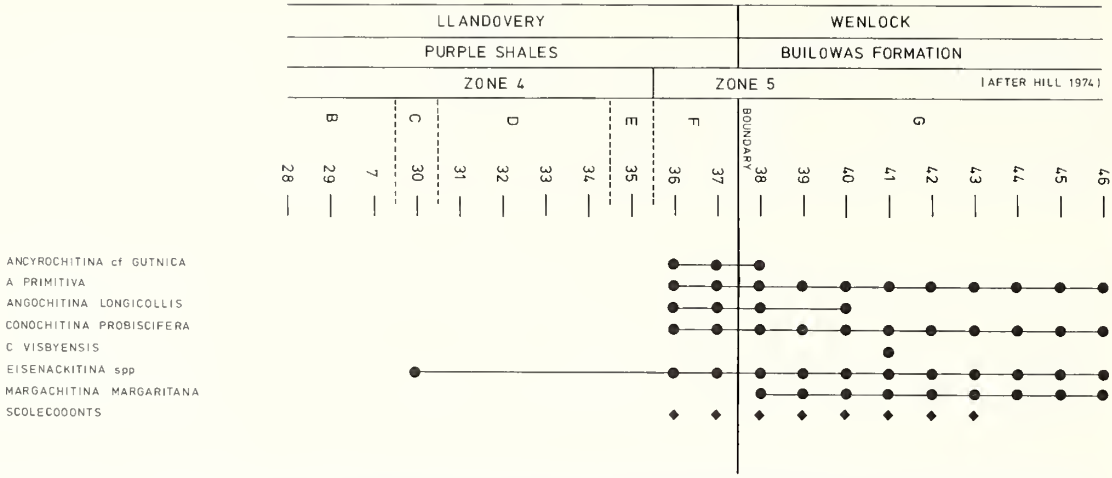
TEXT-FIG. 4. Some acritarch species of restricted stratigraphical distribution in the Llandovery–Wenlock boundary beds, all × 500. *a*, *Deunffia brevispinosa* Downie, sample 25/37, slide 15, co-ordinates Q36/4. *b*, *Domasia amphora* Martin, sample 24/19, slide 4, co-ordinates M35/4. *c*, *Deunffia ramusculosa* Downie, sample 25/36, slide 15, co-ordinates Q31/1. *d*, *D. monospinosa* var. *tonawadensis* Thusu, sample 25/46, slide 4, co-ordinates N49. *e*, *D. furcata* Downie, sample 25/46, slide 4, co-ordinates V51/3. All slides are stored in the collections of the Micropalaeontology Unit, Department of Geology, University of Nottingham.

Almost all of the sixty-two species and varieties of acritarch recorded from the type section have ranges that span the Llandovery-Wenlock boundary. However, the occurrence of stratigraphically restricted species of *Deunffia* and *Domasia* enables the application of the biozonation proposed for this interval by Hill (1974). *Deunffia brevispinosa* Downie, *D. ramusculosa* Downie, and *Domasia amphora* Martin, which appear in the uppermost Purple Shales (unit F), are diagnostic of acritarch zone 5 (Hill 1974). Assemblages from the underlying beds (units B–E) which lack these species, are assigned to zone 4. The base of zone 5 thus occurs about 15 cm below the base of the Wenlock Series in the Leasows section. Within the Buildwas Formation assemblages of zone 5 include *Deunffia monospinosa* var. *tonawadensis* Thusu and *D. furcata* Downie, which is abundant at the top of the section.

Assemblages from the Purple Shales and Buildwas Formation at Domas are almost identical to those from Leasows. Species diagnostic of zone 5 first appear in sample 24/18, although *D. furcata* has not been recorded.

Chitinozoans

With the exception of two specimens of *Eisenackitina* recorded from unit C, chitinozoans occur only in units F and G of the type section (text-fig. 5). Specimens are dark brown to black, compressed, but with appendages well preserved. Most of the recorded species have ranges known to traverse the Llandovery–Wenlock boundary (Aldridge *et al.* 1979; Jenkins and Legault 1979). *Conochitina visbyensis* Laufeld and a number of specimens similar to *Linochitina cingulata* (Eisenack) were found only in the Buildwas Formation. Similar assemblages, with *Eisenackitina* spp., *Sphaerochitina* spp., and *C. probiscifera* Eisenack common, occur at Domas.



TEXT-FIG. 5. Chitinozoan distribution in samples from the stratotype section for the base of the Wenlock Series at Leasows. For the authorship of species see Dorning (1981*b*).

	LLANDOVERY											WENLOCK								
	PURPLE SHALES											BUILDWAS FORMATION								
	B			C	0				E	F		G								
	28	29	7	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
OAPSILODUS OBLIOUICOSTATUS	3	1			6	6	34	9	5	54	15	32	25	11	45	4	3	1	7	15
DECORICONUS FRAGILIS	6	2	3	18	115	67	213	74	37	199	256	256	176	163	197	27	46	7	2	113
PANDERODUS cf RECURVATUS	42	10	3	48	185	76	174	54	29	156	127	249	18							
P LANGKAWIENSIS	25		1	38	127	52	140	53	11	106	73	222	26							
P UNICOSTATUS	224	90	351	127	131	102	127	67	22	138	473	503	198	79	130	15	25	6	3	3
PANDERODUS spp	2	2		9	27	18	27	9	6	13	2	7				2	2			
PSEUOOONEOTOOUS BECKMANNI	27	1	42	5	12	5	25	13	7	19	48	10	4	11	5		2			4
P BICORNIS				11	11	8	29	15	7	6	104	12	7	6	8	2	1	4	3	4
P TRICORNIS	10	13	70	3	19	6	10	3	3	3	16	1								
WALLISERODUS cf CURVATUS		2	9	3	15		25	6	1	32	18	23	17	13	15	2	3	1		
CARNIOOUS CARNULUS	53	26	68	46	`30	171	341	224	134	213	291	22	7							
DISTOMODUS STAUROGNATHOIDES	4	1	31	15	8	7	11	4	5	6	65	12	1							
JOHNOGNATHUS HUODLEI			3	2	4			1	2	1	6									
KOCKELELLA RANULIFORMIS	1	1			2				1	8	2	3								
OULODUS PETILA			5																	
OULODUS sp	5	3	11		1	2			1	1	6	3								
OZARKODINA EXCAVATA	3		5	6	10		11	11	7	18	43	32	9	11	5			3		2
PTEROSPATHOOUS CELLONI	51	22	54																	
P AMORPHOGNATHOIOES				25	134	66	84	64	26	51	153	91	31	6						
P PENNATUS (Pa element)		2	13																	
No of species per sample	14	14	15	14	17	13	14	15	17	17	17	16	12	8	7	6	7	6	4	6

TEXT-FIG. 6. Conodont distribution in samples from the stratotype section for the base of the Wenlock Series at Leasows. All species are multi-element and the numbers given are totals for all elements of each apparatus.

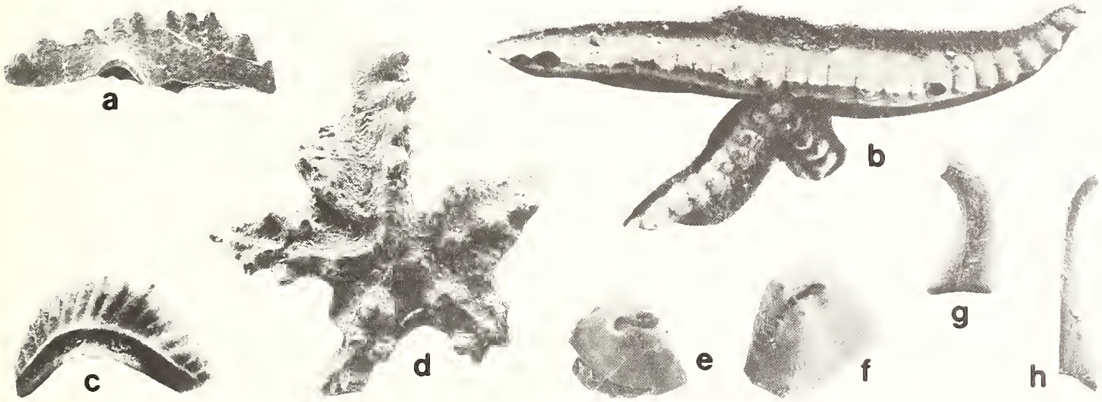
Conodonts

Conodonts were recovered from all lithologies represented in the type section (text-figs. 6, 7). Preservation is good, with discrete elements pale to dark amber in colour. Abundance is moderate to high in the Purple Shales, but falls sharply in the basal Buildwas Formation. More than 18,000 specimens belonging to twenty-one multielement species were examined from Leasows.

Diverse assemblages from the lower beds of the type section (unit B) are characterized by *P. celloni* (Walliser) and *P. pennatus* (Walliser), and are referable to the *celloni* Biozone (Walliser 1964). *P. amorphognathoides* Walliser first appears in sample 25/30 and is the diagnostic species in conodont collections from the uppermost Purple Shales and lowermost Buildwas Formation (unit C to unit G, sample 25/40). The range of *P. amorphognathoides* defines an *amorphognathoides* interval (Aldridge and Mabillard 1981) which may not be fully equivalent to the *amorphognathoides* Biozone defined by Walliser (1964) as the eponymous species of his succeeding zone, *Kockelella patula* Walliser, has not yet been found in Britain. Along with *P. amorphognathoides*, several other species disappear within the lowest beds of the Buildwas Formation, including *Carniodus carnulus* Walliser, *Distomodus staurognathoides* (Walliser), *Panderodus langkawiensis* (Igo and Koike), *P.* cf. *recurvatus* (Rhodes), and *Pseudooneotodus tricornis* Drygant. The succeeding beds bear a considerably diminished fauna, almost exclusively composed of coniform elements, with no additional species making their debut.

The lowest beds exposed at Domas contain conodont faunas with *Pterospathodus amorphognathoides*, and the *celloni* Biozone has not been recognized in the river cliff nor in adjacent strata in the stream bed. *P. amorphognathoides* occurs throughout the Purple Shales and, along with its characteristic associates, is absent in beds of the Buildwas Formation above sample 24/38. The collections from Domas, which contain in excess of 22,000 specimens, are directly comparable in composition with those recognized at Leasows.

We have also examined conodont specimens from samples of the Lower Hill Farm Borehole core, sunk by the Institute of Geological Sciences in 1973 at SO5817 9788, on the outcrop of the Coalbrookdale Formation (see Bassett *et al.* 1975, pp. 4–6). The top of the *amorphognathoides* interval can be recognized at a depth of 239·14 m and the base at 242·21 m; samples from the Purple



TEXT-FIG. 7. Representative elements of some conodont species with restricted stratigraphical ranges in the Llandovery–Wenlock boundary beds, all ×40. *a*, *Pterospathodus celloni* (Walliser), lateral view of Pa element, sample 25/29, BM ×1055. *b*, *P. amorphognathoides* Walliser, upper view of Pa element, sample 24/20, BM ×1056. *c*, *Carniodus carnulus* Walliser, lateral view of Pb? element, sample 24/20, BM ×1057. *d*, *Distomodus staurognathoides* (Walliser), upper view of Pa element, sample 25/7, BM ×1058. *e*, *Pseudooneotodus bicornis* Drygant, upper view of two-tipped, squat, conical element, sample 25/45, BM ×1059. *f*, *P. tricornis* Drygant, upper view of three-tipped, squat, conical element, sample 25/7, BM ×1060. *g*, *Panderodus* cf. P. *recurvatus* (Rhodes), lateral view, sample 25/31, BM ×1061. h, *P. langkawiensis* Igo and Koike, lateral view, sample 25/6, BM ×1062. (All specimens housed in the collections of the British Musuem (Natural History).)

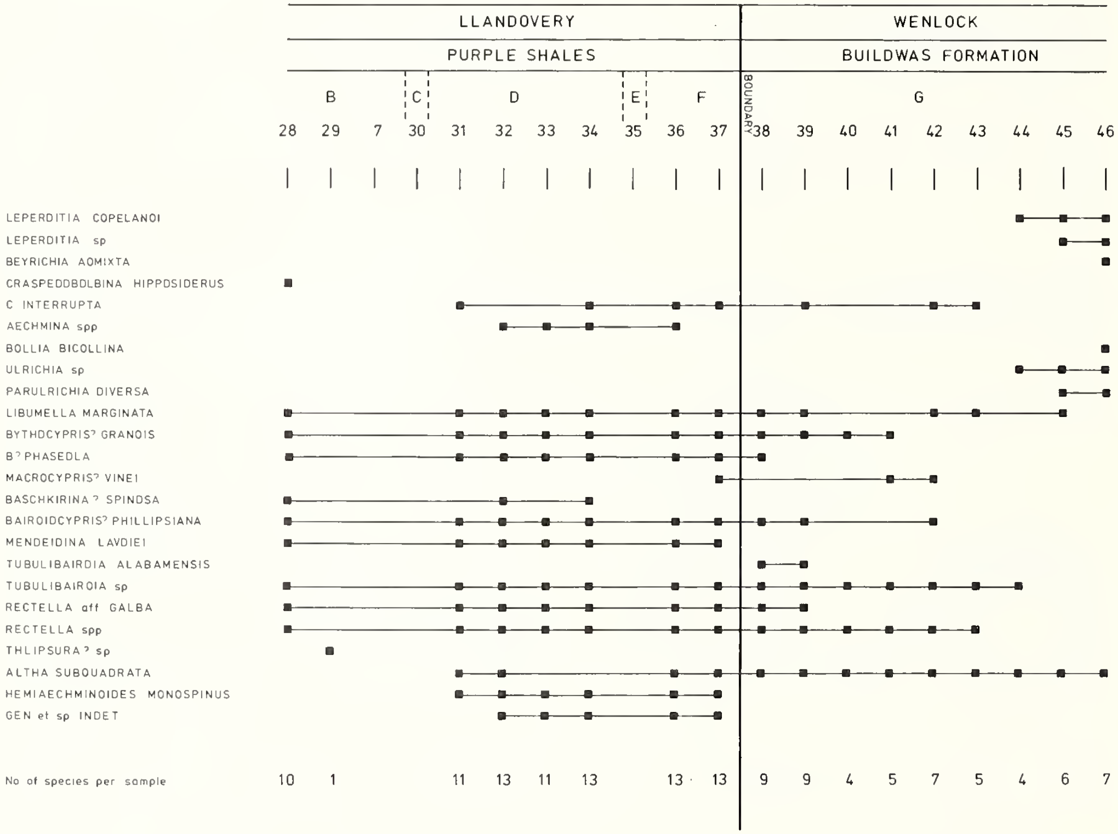
Shales below this contain *P. celloni*. The base of the Buildwas Formation in the core was recorded at 239·69 m by Bassett *et al.* (1975, p. 13).

'*Conodont Pearls*'

Large numbers (more than 8,000 specimens) of small, concentrically laminated, transparent or opaque phosphatic spheres, suspected to be conodont pearls (Glenister *et al.* 1976), were recovered from the Purple Shales (units B–F). In contrast, only sixty-four specimens were recorded from the Buildwas Formation (sample 25/38 at the base of unit G). The decrease in abundance and disappearance of conodont pearls coincides with the disappearance, and possible extinction, of several conodont species. Similar distributions occur at Domas.

Foraminifera

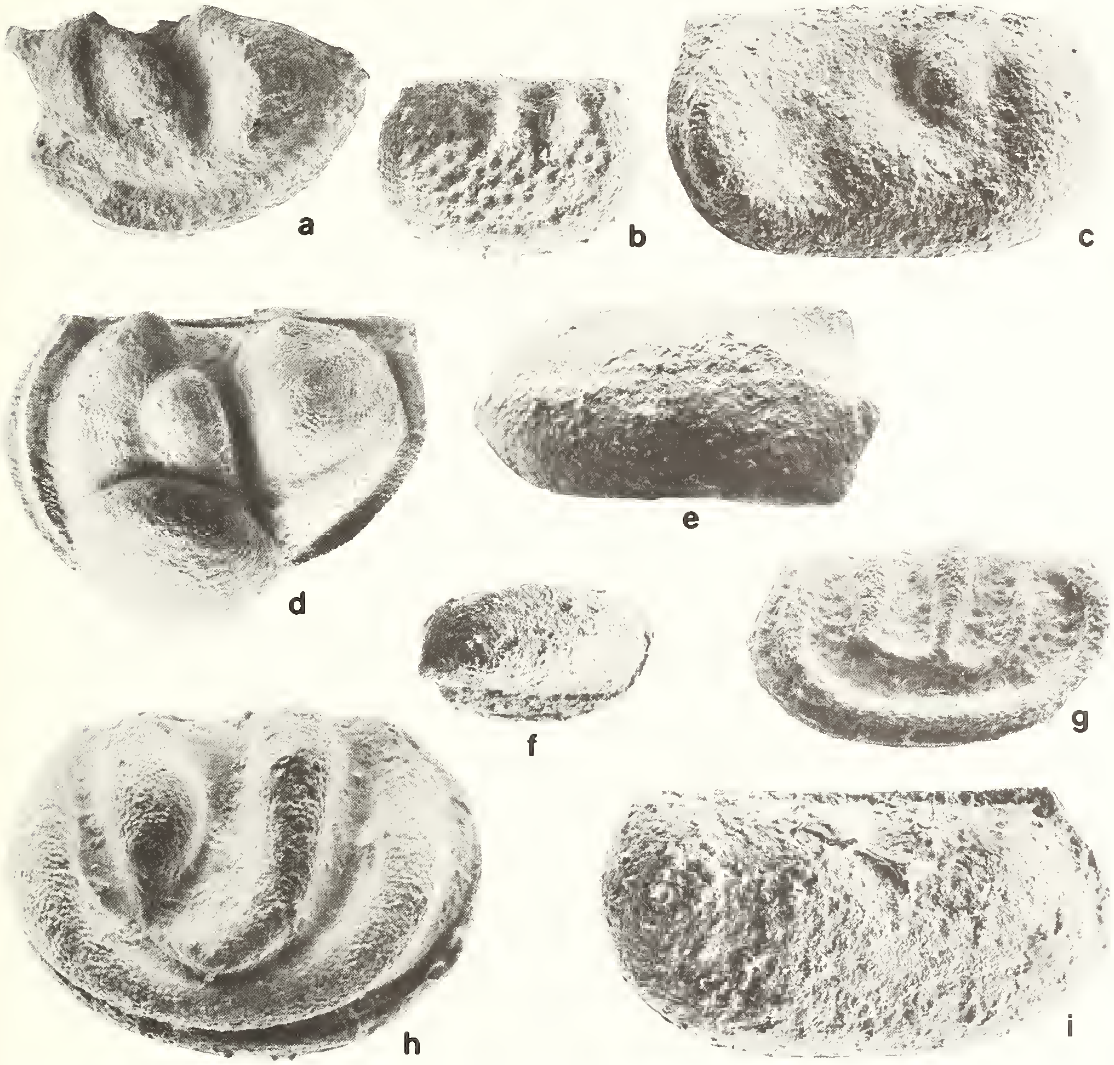
The large numbers of foraminiferans recovered from limestones and shales of the Leasows and Domas sections have been discussed in detail elsewhere (Mabillard and Aldridge 1982). Assemblages from the Purple Shales are dominated by *Ammodiscus exsertus* Cushman, with *Hyperammina* spp., *Webbinelloidea tholus* (Moreman), *Psammosphaera cava* Moreman, and *Hemisphaerammina* sp., and rare *Thurammina irregularis* Moreman and *Turritellella workmani* Dunn. In the basal 20 cm of the Buildwas Formation a faunal change to assemblages of small numbers dominated by *Hyperammina* spp., *Lagenammina* sp., and *Lituotuba* sp. takes place.



TEXT-FIG. 8. Ostracod distribution in samples from the stratotype section for the base of the Wenlock Series at Leasows.

Ostracods

Large numbers of well-preserved ostracods, occurring as carapaces and isolated valves, were recovered from the washings of mudstone samples from both sections (text-figs. 8,9). Limestones contain similar assemblages to adjacent argillaceous beds, but specimens are more difficult to extract and were not examined in detail. Samples from Leasows yielded more than 7,000 specimens



TEXT-FIG. 9. Some ostracod species of restricted stratigraphical distribution in the Llandovery–Wenlock boundary beds. *a*, *Craspedobolbina hipposiderus* Siveter, lateral view of broken left valve, sample 25/28, BM OS12315, ×30. *b*, *Ulrichia* sp., right lateral view, sample 25/46, BM OS12316, ×40. *c*, *Parulrichia diversa* (Jones and Holl), lateral view of right valve, sample 25/46, BM OS12317, ×50. *d*, *C. interrupta* (Jones), left lateral view of female, sample 25/10, BM OS12318, ×30. *e*, *Menoeidina lavoiei* Copeland, dorsal view, sample 25/32, BM OS12319, ×40. *f*, *Rectella* aff. *R. galba* Neckaja, right lateral view, sample 25/34, BM OS12320, ×40. *g*, *Beyrichia admixta* Jones and Holl, left lateral view, sample 25/46, BM OS12321, ×40. *h*, *Bollia bicollina* Jones and Holl, left lateral view, sample 25/46, BM OS12322, ×45. *i*, *Leperditia copelandi* Lundin, sample 25/46, BM OS12323, ×45. (All specimens housed in the collections of the British Museum (Natural History).)

belonging to more than twenty-five species. Abundance is moderate to high in the Purple Shales, becoming moderate to low in the Buildwas Formation.

At Leasows, assemblages from the Purple Shales (units B–F) are dominated by metacopes, particularly species of *Tubulibairdia*. Palaeocopes are represented almost exclusively by *Libumella marginata* Copeland, an oepikellacean. The lowest beds (unit B) are characterized by *Craspedobolbina hipposiderus* Siveter which, together with *Menoeidina lavoiei* Copeland, *Baschkirina*? *spinosa* Copeland, and *Hemiaechminoides monospinus* Morris and Hill, is confined to the Purple Shales. *C. interrupta* (Jones), which is present in the uppermost Purple Shales (unit F), ranges into the Wenlock and is a characteristic component of assemblages in the lowest beds of the Buildwas Formation. Within the basal 70 cm of the Buildwas Formation *Rectella* aff. *galba* Neckaja and other species of *Rectella* disappear. *Bythocypris*? *grandis* (Jones and Holl), *B*? *phaseola* Jones, *Bairdiocypris*? *phillipsiana* (Jones and Holl), *Tubulibairdia* and further species of *Rectella* are also lost, but are known to occur at higher levels in the Wenlock of the type area (Petersen 1975). *T. alabamensis* Lundin is present just above the Llandovery–Wenlock boundary and *Macrocypris*? *vinei* Jones appears slightly higher in the Buildwas Formation. In the highest beds at Leasows, assemblages dominated by *Altha subquadrata* Jones are also characterized by the appearance of *Bollia bicollina* Jones and Holl, *Parulrichia diversa* (Jones and Holl), *Beyrichia admixta* Jones and Holl, *Leperditia copelandi* Lundin, and undescribed species of *Leperditia s.l.* and of *Ulrichia s.l.*

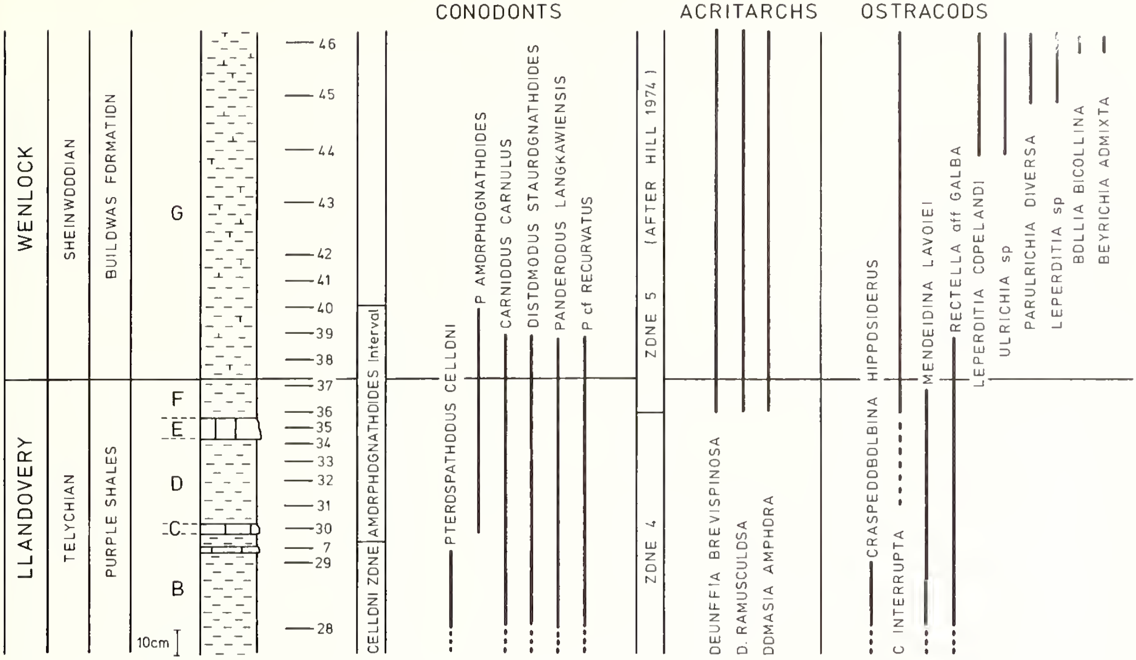
Ostracod collections from Domas comprise more than 12,000 specimens. The assemblages from the Purple Shales are comparable with those from Leasows, but *C. hipposiderus* has not been recognized. The assemblages identified in the lowermost Buildwas Formation at Leasows are also present at Domas, but the palaeocope fauna that characterizes the uppermost beds collected in the type section is not represented in the Domas exposure.

BIOSTRATIGRAPHY

Several species of acritarchs, conodonts, and ostracods have stratigraphically restricted distributions in the sections studied and are of value in delimiting the base of the Wenlock Series (text-fig. 10). The acritarchs *Deunffia brevispinosa*, *D. ramusculosa*, and *Domasia amphora* appear in uppermost Llandovery strata (unit F at Leasows), with their stratigraphic base in the type area coincident with a change in lithofacies that may offer an improved potential for preservation. However, their ranges also begin within the *amorphognathoides* conodont interval elsewhere in the Welsh Borderland, and they seem to offer a good basis for correlation. Conodont faunas do not appear to have been affected by the lithofacies changes in the latest Llandovery, and the base of the *amorphognathoides* biozone, recognized at 65 cm below the base of the Wenlock at Leasows, provides an excellent datum for correlation. The local extinction of *Pterospathodus amorphognathoides*, 30 cm above the base of the Wenlock at Leasows, may be a less reliable event, but the disappearance of this species along with several others in the lowest Wenlock is widely recognized (Aldridge 1976).

Several ostracod species have apparently restricted distributions in the type area, but most are undescribed or poorly known and their biostratigraphical value cannot be assessed. Palaeocope species, especially of the genus *Craspedobolbina*, are the most useful, with *C. hipposiderus* occurring in the lower beds (unit B) at Leasows, succeeded by *C. interrupta*, which spans the Llandovery–Wenlock boundary. *Parulrichia diversa*, *Bollia bicollina*, and *Beyrichia admixta* are known only from the Wenlock (Siveter 1978).

The base of the Wenlock Series at Leasows cannot so far be shown to be coincident with the base of any biozone, microfossil or macrofossil, and its position in other sections can only be assessed through establishing the local ranges of species known to be of restricted distribution in the type area. It is wise to use information from as many groups as possible, but at present a combination of acritarch and conodont ranges provides the best basis for correlation. Thus, the Llandovery–Wenlock boundary lies within the *amorphognathoides* conodont interval, between the base of acritarch zone 5 and the disappearance of *Pterospathodus amorphognathoides*; these horizons are separated by approximately 40 cm of strata in the type section. At Domas, in the type area, the same interval is



TEXT-FIG. 10. Ranges at Leasows of selected microfossil taxa of value in correlating the base of the Wenlock Series.

represented by approximately 90 cm of strata. On a somewhat broader scale, conodonts alone allow a guide to correlation, with the *amorphognathoides* interval spanning the Llandovery-Wenlock boundary and restricted to a thickness of 95 cm of strata in the type section. It is important to note, however, that this interval is represented in much greater thicknesses elsewhere. At Domas, only 4 km from Leasows, the base of the *amorphognathoides* biozone is not exposed but the species ranges through 2 m of the available section, and in the Lower Hill Farm Borehole, little more than 1 km from Leasows, the stratigraphical thickness representing the *amorphognathoides* interval is approximately 3 m. In the Coralliferous Group of Marloes Bay, south-west Dyfed, Wales, the *amorphognathoides* interval occupies at least 40 m of strata (Mabillard and Aldridge 1983) and in the Ringerike District of the Oslo Region, Norway, it occurs through 30 m (Worsley *et al.* 1983). Thus, in areas of rapid sedimentation, it may only be possible to delimit the base of the Wenlock rather broadly even when several fossil groups are taken into account. However, determinations may be improved somewhat when macrofossil distributions in the type section have been documented in the same detail as we have provided for the microfossils.

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THE FIRST MESOZOIC CHONDROPHORINE (MEDUSOID HYDROZOAN), FROM THE LOWER CRETACEOUS OF JAPAN

by GEORGE D. STANLEY, JR. *and* YASUMITSU KANIE

ABSTRACT. Floating jellyfish-like hydrozoans belonging to the Suborder Chondrophorina are a little known but distinctive group extending back to the Precambrian with sporadic occurrences in the Palaeozoic. Their absence from post-Carboniferous rocks was puzzling, considering their abundance and wide distribution today. *Palaelophacmaea annulata* (Yokoyama), from the lower Cretaceous (Barremian) of Japan, is reinterpreted as the first known example of a chondrophorine fossil from the Mesozoic. The species was previously considered to be a patelliform gastropod. The remarkable similarity of chondrophorine pneumatophores to some univalved molluscs complicates precise indentification. Possible criteria to aid in distinguishing these little-known fossils are discussed.

CHONDROPHORINES are floating jellyfish-like hydrozoans represented in today's oceans by the widely distributed *Velella* and *Porpita*. *Velella* employs a fixed sail as its principal means of propulsion and such open-sea mariners are accordingly referred to as 'by-the-wind sailors'. Whole flotillas of these organisms are frequently driven onshore by strong wind. *Porpita*, another chondrophorine, lacks a sail but follows a similar planktonic life-style. Details of the anatomy and ecology of both organisms were given by Hyman (1940).

Although thought of as soft-bodied jellyfish, chondrophorines actually secrete within their coenosarcal tissues a tough, gas-filled, chitinoid float structure, the pneumatophore. In *Velella* these convex structures consist of a concentric series of closely adpressed gas chambers that frequently wash up in great abundance on many beaches. Such pneumatophores are hard but flexible and possess some potential for preservation. As demonstrated for some well-preserved Devonian examples, the disc-shaped pneumatophore can provide a hard surface for the attachment of epifauna (Yochelson *et al.* 1983). Sinking, burial, and compression of the concentric gas chambers may produce fossils strikingly reminiscent of some mollusc shells.

The conservative nature of chondrophorine evolution is readily apparent when Silurian or even Precambrian (Wade 1971) examples are compared with their living counterparts. During their long existence, they have undergone very little elaboration of their basic morphology. *Plectodiscus* Ruedemann, for example, is similar in both hard and soft parts to living *Velella* and ranges from late Silurian to middle Pennsylvanian with little morphological change.

Although abundant today, the fossil record of chondrophorines is exceedingly sparse and sporadic. Only sixteen occurrences have been reported, ranging from the late Precambrian Ediacara fauna to the Carboniferous (Stanley 1982). Despite extensive palaeontological investigations of post-Carboniferous strata, no examples have been reported previously. The apparent absence of chondrophorines during this 300 MY interval is very puzzling.

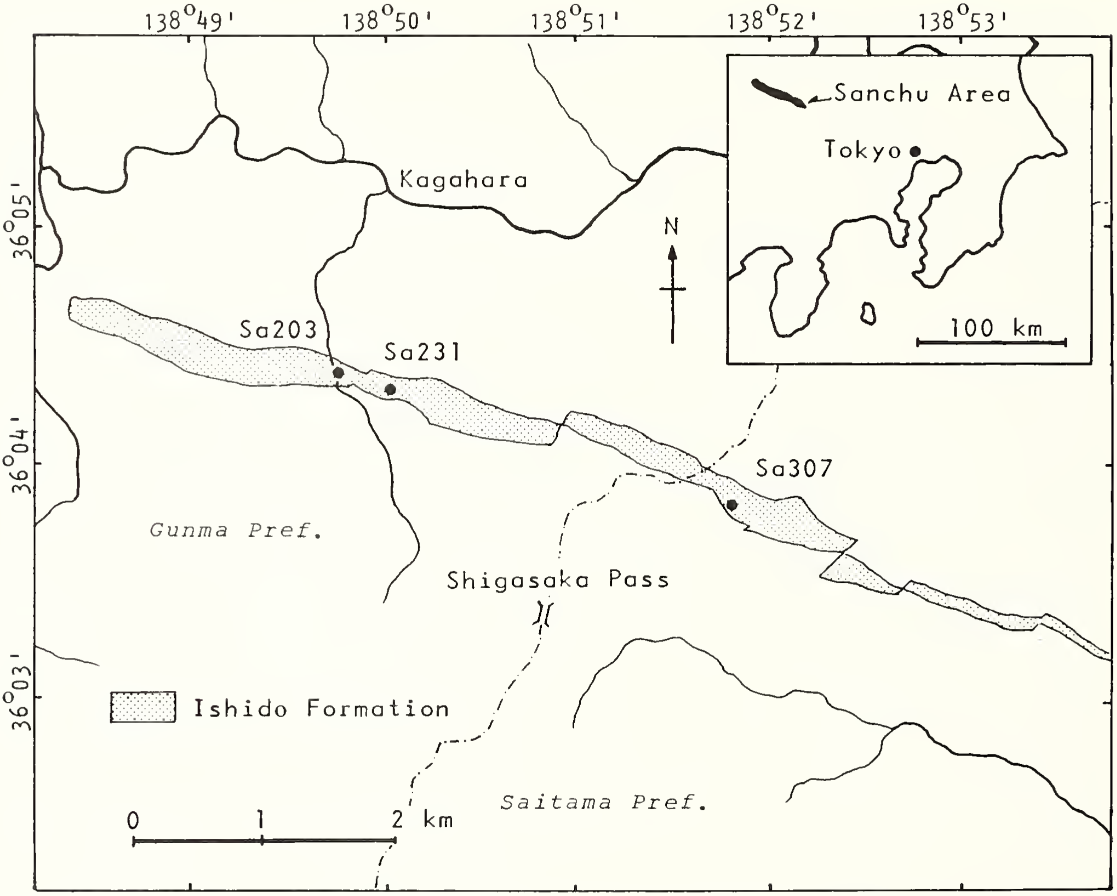
We describe the first post-Carboniferous chondrophorine which comes from the lower Cretaceous of Japan and appears related to earlier examples in the lower Ordovician and Precambrian. Previously classified as molluscs, these fossils are now identified as chondrophorines.

[Palaeontology, Vol. 28, Part 1, 1985, pp. 101-109, pl. 10.]

STRATIGRAPHY AND PALAEOECOLOGY

Stratigraphic occurrence

The chondrophorine comes from localities Sa203, Sa231, Sa307 (text-fig. 1). It occurs in the upper part of the Ishido Formation in the Sanchu area of Japan (text-fig. 2). The specimens were collected by M. Matsukawa and K. Takei during geologic studies in the Sanchu area. The Ishido Formation is a fining-upwards sequence, with coarse-grained deposits grading upwards into fine-grained sandstone, which locally alternates with black shale. Localities Sa203 and Sa231 (text-fig. 1) consist of very fine-grained calcareous sandstone and locality Sa307 is composed of very fine-grained calcareous sandstone and black shale. According to Matsukawa (1977), the fossil localities in the upper fine-grained facies of the Ishido Formation are generally of muddy facies.


138°49'
138°50'
138°51'
138°52'
138°53'
36°05'
36°04'
36°03'
Sanchu Area
Tokyo
100 km
Kagahara
N
Sa203
Sa231
Sa307
Gunma Pref.
Shigasaka Pass
Ishido Formation
0
1
2 km
Saitama Pref.

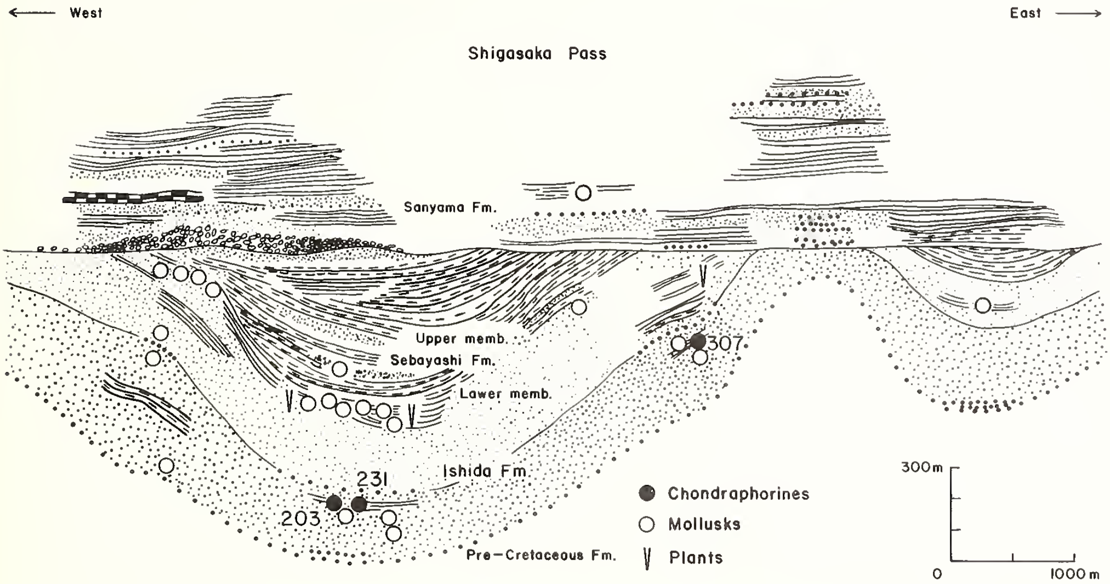
TEXT-FIG. 1. Locality map of the Sanchu area of Japan showing locations of chondrophorine fossils described in text. Numbers refer to localities.

Geological age

According to Obata *et al.* (1976), the upper part of the Ishido Formation is upper Barremian in age as shown by the occurrence of the ammonites *Barremites* (*Barremites*) aff. *strettostoma* (Uhlig), *Heteroceras* (*Heteroceras*) aff. *astieri* D'Orbigny, and *Pseudohaploceras otsukai* (Yabe and Nagao).

Palaeoecology and associated fauna

Locality Sa307 yields abundant bivalves: *Astarte* (*Astarte*) *subsenecta*, *A.* (*Yabea*) *shinanoensis*, *Entolium sanchuensis*, *Gervillaria haradae*, *Grammatodon* (*Nanonavis*) *yokoyamai*, *Pterotrigonia* (*Pterotrigonia*) *hokkaidoana*, *P.* (*P.*) *pociliformis*, *Lycettia* sp., undetermined species of scaphopods, and one species of ammonite *Barremites* (*Barremites*) sp. Many trigoniid bivalves occur in direct association with the chondrophorines. Numano and Nakano (1965) interpreted *Pterotrigonia* as inhabiting calm bottoms somewhat offshore. Alternatively, Tashiro and Matsuda (1982) viewed this bivalve as inhabiting a shallow sea near the tidal zone.



TEXT-FIG. 2. Geological cross-section showing the stratigraphic succession of Cretaceous rocks in the eastern part of the Sanchu 'Graben' and location of fossils including chondrophorine (after Matsukawa 1977).

Locality Sa203 contains nine taxa of uncoiled ammonites: *Kabylites* (?), *Acrioceras* aff. *tabarelli*, *Lytocrioceras* (?) *furcatum*, *L.* (?) sp., *Hamiticeras* (?) sp., *Heteroceras* sp., *H.* (?) sp., *Anahamulina* aff. *subcylindrica*, *A.* sp.; seven species of coiled ammonities: *Phyllopachyceras* aff. *infundibulum*, *Calliphylloceras* (?) sp., *Aconeceras* sp., *Barremites* (*Barremites*) aff. *strettostoma*, *B.* (*B.*) aff. *difficilis*, *B.* (*B.*) sp., *Pseudohaploceras* (?) *otsukai*, and one species of nautiloid *Cymatoceras* aff. *neocomiensis*. The depth distributions of the Barremian species of phylloceratids, ancyloceratids, ptychoceratids, desmoceratids, and oppelliids are uncertain. We infer depth distributions of these ammonites in the infraneritic zone between 36 and 180 m (Scott 1940) or in an intermediate facies between inshore shallow water and offshore deep water, based on the abundant occurrences of heteromorphic ammonites (Tanabe 1979).

Environment of deposition

The Ishido Formation is regarded as a transgressive deposit with a basal conglomerate. The upper part of the Ishido Formation yielding the chondrophorines represents a fine-grained, 'muddy' facies. Sandstone of the Ishido Formation in the northern sub-belts is characterized largely by a feldspathic greywacke, the clasts composed largely of chert (Takei 1980). These deposits received sediment from the north and the sedimentary basin is thought to have been close to land areas and of moderate depth. The interval yielding the chondrophorine fossil is a quiet water, transgressive stage and both palaeontological and sedimentological data are consistent with a shallow-water, predominantly fine-grained clastic sediment substrate.

PRESERVATION AND TAPHONOMY

A review of the small number of Palaeozoic chondrophorine occurrences shows that depending on the original shape, nature of enclosing sediments, and type of preservation, the configuration of the pneumatophore or disc can vary from totally flattened to a strong, cap-like convexity (Stanley 1982). After some post-mortem floating, their gas-filled pneumatophores presumably became waterlogged and sank. Abundant remains of a whole flotilla of fossil velellids have been reported from deep basinal rocks of early Carboniferous age (Stanley and Yancey in press), but examples of very shallow-water origin are also known (Yochelson and Stanley 1981). Living *Velella* occurs in great concentrations and is frequently driven landward by prevailing winds to become beached and concentrated on the strand line (Yochelson *et al.* 1983). Thus chondrophorine remains would be expected to occur throughout a wide variety of near-shore to offshore facies types and they may be locally concentrated.

The rarity of the Ishido specimens, coupled with their occurrence in relatively near-shore facies of presumed low-energy and moderate depth, suggests that these chondrophorines did not become beached but sank individually, in quiet waters a short distance offshore. The vague concentric outlines and convex shapes of some of the pneumatophores (Pl. 10, fig. 2) may have resulted from infilling of pneumatocyst chambers by fine-grained sediment before compression occurred.

SYSTEMATIC PALAEONTOLOGY

Phylum CNIDARIA Haeckel, 1881
Class HYDROZOA Owen, 1843
Order HYDROIDA Johnston, 1836
Suborder CHONDROPHORINA Chamisso and Eysenhardt, 1821
Family CHONDROPLIDAE Wade, 1971
Genus PALAELOPHACMAEA Donaldson, 1962

Type species. Palaelophacmaea criola Donaldson, 1962.

Diagnosis. Subcircular low cone with distinct radial ridge extending to margin and irregular concentric corrugations with finer growth lines on each. No indication of sail structure.

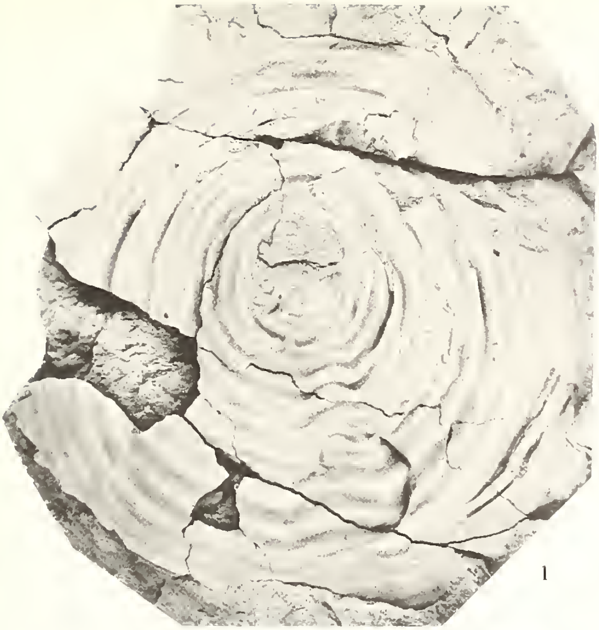
Palaelophacmaea annulata (Yokoyama)

Plate 10, figs. 1–6

1890 *Capulus annulatus* Yokoyama, pl. 25, fig. 17*a*, *b*.
1963 *Brunonia* ? *annulata* (Yokoyama); Matsumoto *et al.*, pl. 51, fig. 17.
1975 *Anisomyon annulatus* (Yokoyama); Kanie, pl. 19, figs. 3, 4*a*, *b*.
1977 *Anisomyon annulatus* (Yokoyama); Kanie, pl. 2, fig. 7.

EXPLANATION OF PLATE 10

Figs. 1–6. *Palaelophacmaea annulata* (Yokoyama), Ishido Formation. All specimens whitened with MgO. 1, NSM PM1246a, cast showing low, flattened shape and irregular but concentric corrugations interpreted as flattened pneumatocysts. Note original radial ridge is also flattened to produce a furrow, × 1·2, Loc. Sa307. 2, YCM GP548, × 1, loc. Sa203. 3, YCM GP552, small, oval specimen showing concentric corrugations but without any clear signs of a radial ridge, × 1·66, loc. Sa203. 4, NSM PM1249, details of central area and suspected central pore. Note coarse pustulose granules, × 2·2, loc. Sa231. 5. NSM PM1249, almost complete, highly convex specimen, illustrating the distinct radial ridge and central apex. Note finer 'growth lines' and irregular outer margin characterized by flexure of the lower left side, × 1·25, loc. Sa231. 6, YCM. GP549, illustrating the irregularities of the concentric pneumatophore, offset radial ridge, and irregularities of the margin, × 2, loc. Sa203.



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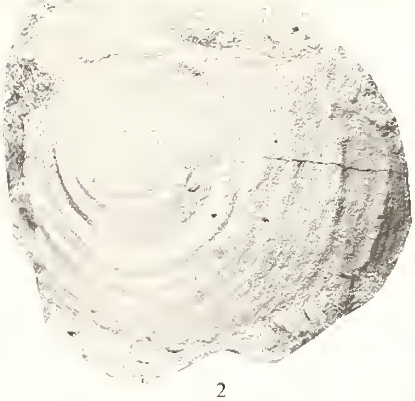

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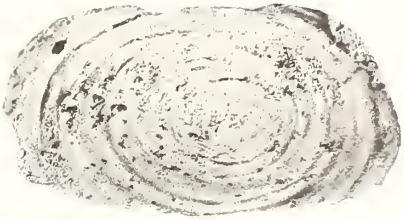

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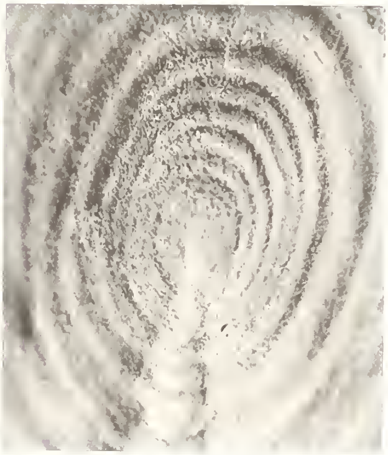

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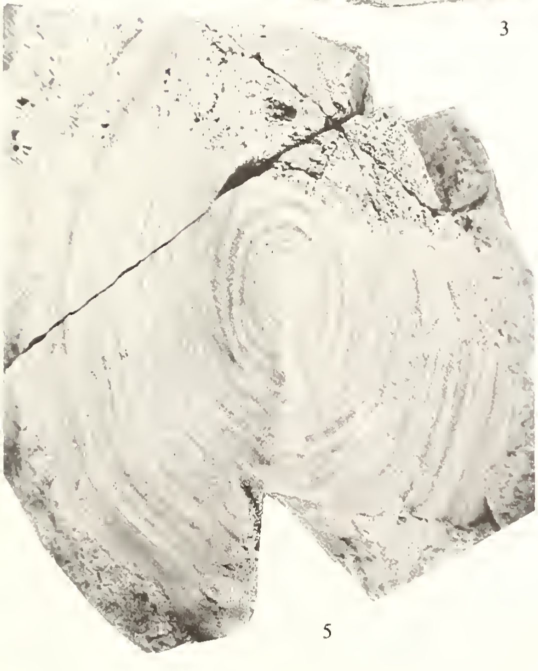

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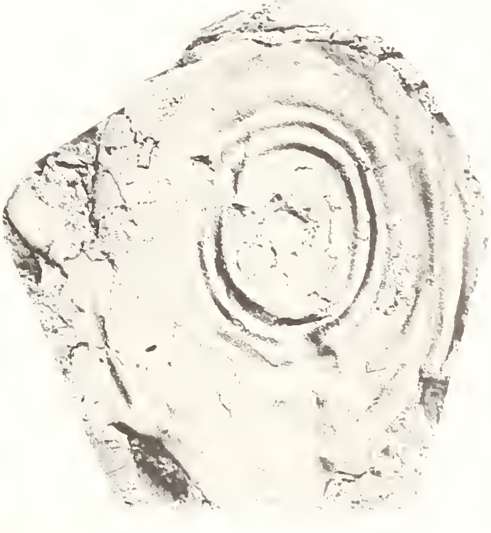

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STANLEY and KANIE, *Palaelophacmaea*

Material. Description based on five well-preserved specimens showing both interior and exterior: YCM GP548, YCM GP549, YCM GP552, NSM PM1246 a, b, and NSM PM1249, housed in the National Science Museum (NSM), Tokyo and in the Yokosuka City Museum (YCM), Yokosuka, Japan.

Description. Low, circular to oval bilateral shields or cones, 1–3 cm high with irregularly spaced concentric corrugations (pneumatocysts) ending in sharp apical ring. Pneumatocysts slightly overlapping and 1–3 mm thick. Finer concentric lines superimposed on pneumatocysts, about five to twenty on each one. Pneumatophore disc usually thin and compressed with a distinct, raised radial ridge extending from apex to margin to produce bilateral symmetry. A very faint, fine granular texture occurs over surface of most fossils while others are smooth, suggesting that a thin film-like covering was present. Outer margin flat and irregular, possibly deflected at contact with radial ridge.

Discussion. One of us (Y.K.), has examined the type of Yokoyama (Bayerische Staatssammlung, Munich, West Germany) and found that it agrees precisely with our material. The most distinctive aspects of the specimens are the radial ridge and somewhat irregularly arranged, concentric corrugations of the pneumatophore disc. The preserved configuration of the disc ranges from conical to flattened depending on the degree of compression. The expanding radial ridge is plastically deformed and offset in one specimen (Pl. 10, fig. 6) suggesting an originally chitinous pneumatophore. Another specimen (Pl. 10, fig. 2) shows coarse, less distinct corrugations and surface details, suggesting that it is an interior cast of the pneumatocysts. All specimens show some distortion, especially flattening. Plate 10, figs. 4, 5 show a complete, centrally located, sharp apex formed by a single ring-like corrugation and central pore. The surface is characterized by a fine pustulose texture with finer lines superimposed on the broader corrugations of each pneumatocyst. One broken specimen (Pl. 10, fig. 1) shows a smooth, thin, almost film-like surface.

SYSTEMATIC POSITION AND AFFINITIES

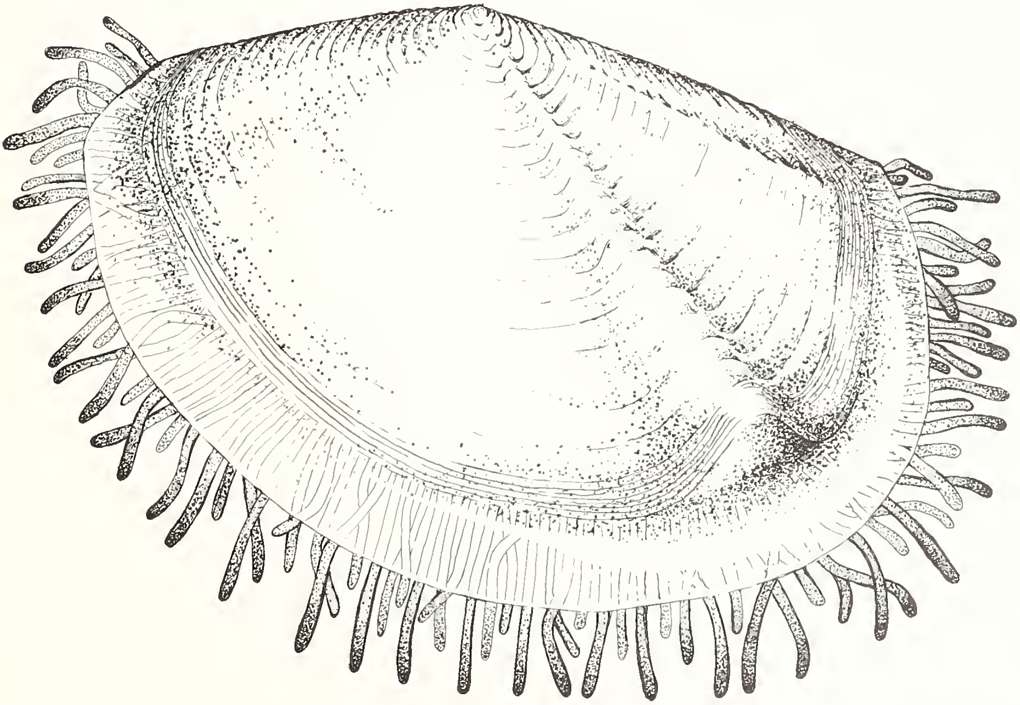
The species *Anisomyon annulatus* was described as a patelliform gastropod by Yokoyama (1890, p. 200, pl. 25, figs. 1–7*a*, *b*) and originally designated *Capulus annulatus*. Yokoyama's specimen was again illustrated as a patelliform gastropod by Matsumoto *et al.* (1963) and conspecific material was similarly described and illustrated by Kanie (1975, 1977). Based on our re-evaluation of these specimens, all the fossils of this species must be transferred from Mollusca to Cnidaria (Hydrozoa).

Palaelophacmaea was described by Donaldson (1962) as an enigmatic limpet-like patelliform gastropod from the lower Ordovician of central Pennsylvania, U.S.A. (type species *P. criola* Donaldson). Donaldson's specimens were reillustrated by Yochelson and Stanley (1981) and on the basis of comparative study with Devonian chondrophorines, they assigned *Palaelophacmaea* to the chondrophorine hydrozoans. The similarity between Donaldson's specimens and *A. annulatus* (Yokoyama) is so striking in all aspects that we are forced to reassign this species to *Palaelophacmaea*. As outlined in Yochelson and Stanley (1981) features such as the irregularity of the concentric corrugations, evidence of plastic deformation, and the thin, film-like nature of the 'shell' are not characteristic of a mollusc shell but more compatible with the convex, internal, chitinoid pneumatophore of a chondrophorine hydrozoan. Although fossil chondrophorines were first recognized by Ruedemann (1916), details of these fossils were not known until the work of Caster (1942). They are still usually regarded either as problematica or confused with a variety of unrelated organisms. The apparent similarity of their compressed float structure with univalved mollusc shells is particularly striking.

Kanie (1975, pp. 27–29, pl. 19, figs. 3 and 4*a*, *b*; 1977, pl. 2, fig. 7) described and illustrated specimens of *A. annulatus* (Yokoyama) in a monograph and paper on Cretaceous patelliform gastropods from the northern Pacific and compared them with the type illustrated in Matsumoto *et al.* (1963). Kanie (1975) noted the unusual thinness of the shell and the absence of muscle scars in all specimens of *A. annulatus*. In discussing the relationship with other Cretaceous species of patelliform gastropods, Kanie (1977, p. 60) noted the questionable nature of Yokoyama's specimen.

Absence of muscle scars is an important criterion for distinguishing the chondrophorine pneumatophore from the shells of univalved molluscs. Yochelson *et al.* (1983) reviewed the biology and anatomy of lower Devonian chondrophorines, providing additional clues for their recognition. These include: (1) evidence of plastic deformation of the originally pliable chitinoid pneumatophore which is readily subject to deformation, especially crushing, without fracturing, (2) irregularities of the concentric corrugations and the distinctive radial ridge or groove, and (3) the exceedingly thin nature of the compressed pneumatophore which is quite different from thicker, calcitic material of mollusc shells. In addition to the above criteria, the occurrence of suspect fossils in environments generally uncharacteristic for some molluscs, such as deep pelagic sediments, might also prove useful. Chondrophorines, being planktonic wind-dispersed organisms, can occur in all facies types, but most frequently occur in association with exclusively pelagic or deeper water benthic faunas.

P. criola and *P. annulata* differ from all other taxa and cannot be assigned to either of the two chondrophorine families Velellidae and Porpitidae (Harrington and Moore 1956). The Velellidae, such as *Plectodiscus*, like *Palaelophacmaea* are bilaterally symmetrical but display a distinct sail rising from the pneumatophore disc or cone. The Porpitidae, on the other hand, lack a sail and are radially, not bilaterally, symmetrical by virtue of numerous radial partitions within the circular pneumatophore. *P. annulata* and *P. criola* lack a sail but they possess bilateral symmetry and concentric pneumatocysts rather than radial partitions like the Porpitidae (text-fig. 3). The raised ridge of *P. annulata* is not a structure homologous with the velellid sail but, like other chondrophorines, most likely accommodated a major vascular vessel that crossed the soft



TEXT-FIG. 3. Reconstruction of *Palaelophacmaea annulata* shown in floating position. Reconstruction illustrates the convex pneumatophore disc that during life was secreted within the coenosarcal tissues of the hydrozoan. Arrangement and positions of the tentacles and other soft parts is based on those of *Porpita* and *Velella*.

coenosarcal tissues in which it was imbedded. Although characteristics of *P. annulata* do not allow its placement in any living chondrophorine family, they do agree with Precambrian bilaterally symmetrical chondrophorines from the Ediacara fauna for which Wade (1971) erected the family Chondroplidae. We therefore assign *P. annulata* to this extinct family. In doing so we not only establish *P. annulata* as the first Mesozoic chondrophorine, but also extend the range of the family from the Pre-Cambrian to the Cretaceous, with only one other occurrence in the Ordovician (Yochelson and Stanley 1981). Continued search may reveal further examples within this extensive interval of time. This still leaves open the question of why representatives of the two extant families, Porpitidae and Velellidae, have not yet been found in post-Carboniferous strata. Because few palaeontologists are familiar with these fossils, discovery and proper identification of other examples hinges on understanding conventional chondrophorine morphology and establishing multiple, working criteria to distinguish such fossils from morphologically similar but unrelated molluscan taxa. Based on the conservative nature of their evolution and their wide stratigraphic range, one should expect to find closely similar genera and species occurring throughout the Phanerozoic.

Acknowledgements. We thank Mr. K. Takei (Kosei High School, Tokyo), Dr. M. Matsukawa (Ehime University), and Mr. H. Tsuda for collecting and donating the chondrophorine specimens for our study. Dr. E. L. Yochelson first recognized the problematic nature of our specimens and the possibility that they could be chondrophorine pneumatophores rather than univalved molluscs. We are grateful to him for earlier discussions concerning the affinities of our material as well as reviewing an earlier draft of our manuscript. Ms. R. Jumer (Missoula) skilfully drafted the reconstruction in text-fig. 3.

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NOTE ADDED IN PROOF

Additional specimens from the Ishido Formation described as *Brunonia annulata* (Yokoyama) and as a new species *B. undulata* Kase, appeared in publication while this paper was in press. The former specimens (Kase 1984, pl. 3, figs. 8–10) are judged by us to be *Palaelophacmaea annulata* (Yokoyama). The latter (Kase 1984, pl. 3, figs. 6*a*, *b*, 7*a*, *b*) may also be referred to *Palaelophacmaea*.

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THE PERMIAN LYCOPOD *CYCLODENDRON LESLII* FROM SOUTH AFRICA

by R. J. RAYNER

ABSTRACT. Well-preserved axes of the southern hemisphere Permian lycopod *Cyclodendron leslii* (Seward, 1903) are described from localities in South Africa. New information includes details of the cuticle with stomata, epidermal cells, leafy vegetative axes, and fertile axes. *C. leslii* was an arborescent heterosporous lycopod with a restricted stratigraphic range, and it formed a small but significant part of the *Glossopteris* flora of South Africa.

IMPRESSION fossils from Vereeniging, Atherstone Quarry, and Port Alfred, South Africa, were described by Seward (1903) under the name *Bothrodendron leslii.* He noted dichotomous branching of leafless axes and variation in size, frequency, and appearance of leaf scars; his choice of genus was influenced by a strong resemblance of the South African material to *B. kiltorkense* from Ireland. The Vereeniging material was later figured by Arber (1905) who formalized a diagnosis of *B. leslii.* The assignment of these axes to a northern hemisphere genus was not altogether popular, leading Kräusel (1928) to erect a new genus *Cyclodendron*, based upon well-preserved leafy material from the Ecca beds in South West Africa; he also included Ugandan material and the specimens previously described by Seward (1903). Du Toit (1932) accepted the validity of Kräusel's genus and gave a comprehensive account of the vegetative axes of Ugandan *Cyclodendron.* In discussing the geographical distribution of *C. leslii* (Vereeniging, Vierfontein, (?)Newcastle, Goamus, Wankie, east Tanganyika, Lukuga, and west Lake Tanganyika) in the Karoo beds of Africa, du Toit (1932) pointed out the limited stratigraphic range of the species. The monospecific genus seemed secure; it had a characteristic morphology and was considered to be geographically and stratigraphically restricted.

Edwards (1952), however, re-examined the southern hemisphere lycopods housed in the British Museum (Natural History) and followed White (1908) by placing them all in the Brazilian species *Lycopodiopis pedroanum*, a species characterized by the absence of both a central leaf scar and parichnos scars. The Brazilian specimens of *L. pedroanum* have been recently redescribed as *Brasilodendron pedroanum* by Chaloner *et al.* (1979). The former name is now reserved for permineralized material showing internal anatomy, while the latter is used for material with preserved outer morphology.

The taxonomic arguments over the treatment of southern hemisphere Permian lycopods were partially resolved by Kräusel (1961) who illustrated and described a fertile *Cyclodendron* axis. Subsequent authors, however, have not been consistent in their identification of *C. leslii* from Africa (e.g. compare Plumstead 1961 and 1973); the genus requires thorough description, particularly of details of fertile organization. New collections from several localities within the Ecca sediments have revealed details of fertile axes, leaf morphology, and cuticle that show *Cyclodendron* to be a distinctive genus, differing significantly from other coeval southern and northern hemisphere lycopods.

MATERIALS AND METHODS

This paper is based on fossil plants found at two Permian localities, Vereeniging and Hammanskraal, South Africa. Three authors have worked on parts of the well-preserved Hammanskraal assemblage: Plumstead (1969) described two large fructifications; Kovács-Endrödy (1974, 1976) reported fertile and vegetative *Glossopteris* leaves; and Smithies (1978) reviewed the complete assemblage. Their material, and the specimens described in

[Palaeontology, Vol. 28, Part 1, 1985, pp. 111–120, pls. 11–13.]

this paper, were collected from a disused refractory brick quarry about 7 km south of Hammanskraal in the central part of Transvaal Province. The fossils are coalified compressions (*sensu* Schopf 1975), some with cuticle.

Large numbers of plant fossils from the Vereeniging locality are housed at the Bernard Price Institute, University of Witwatersrand, Johannesburg; attached glossopterid fructifications were discovered among them and described by Plumstead (1952), while I have found and described here a number of impressions of fertile *Cyclodendron* axes. The locality has been thoroughly described by le Roux and Anderson (1977). The *Cyclodendron* axes are preserved either as endocortical casts or impressions in a very fine-grained matrix. Chaloner *et al.* (1980) reviewed this form of preservation where, after burial and presumed partial decomposition of tissues, mud infilled a cortical cavity. Subsequent compression and collapse of the plant tissues produced a cast of the mud infill. Leaves are exclusively impressions while axes are both endocortical casts and impressions of casts in the matrix. The outer surface of the stem cast closely resembles the original plant surface because the matrix is so fine grained. Indeed, the outline of some epidermal cells is preserved, presumably as an impression of the inner surface of the cuticle on the mud infill prior to consolidation of the sediment. No organic matter remains but the specimens are invaluable in providing details of gross morphology of leaves, leaf scars, and fertile axes.

Macrospecimens, both impressions and compressions, were uncovered using steel needles ('dégagement' of Leclercq 1960). The specimens were repeatedly photographed during development. Impression fossils were photographed under unidirectional lighting. Portions of well-preserved impressions showing features of the epidermis were mounted on stubs for scanning electron microscopy. Cuticles were carefully removed from the Hammanskraal coalified compressions with a fine brush, oxidized with Schulze, neutralized in dilute alkali, washed, and mounted on glass slides or directly on to SEM stubs. Photomicrographs were taken on Wild M8 (incident light) and Zeiss (transmitted light) microscopes.

Smithies (1978) reviewed several of the Ecca plant-bearing localities and, on macroplant evidence, placed both Vereeniging and Hammanskraal in Plumstead's (1966) floristic zone III or basal IV with a lower Permian age. Anderson (1977) studied the palynology of Hammanskraal and placed the assemblage in the middle Ecca, also with a lower Permian age.

All specimens are housed in the Bernard Price Institute (BP).

SYSTEMATIC PALAEONTOLOGY

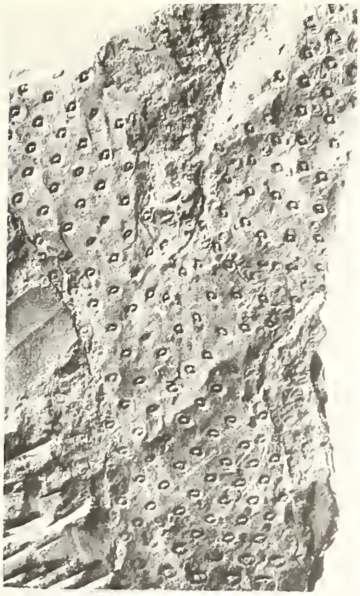
Division TRACHEOPHYTA
Class LYCOPSIDA
Order LEPIDODENDRALES
Family LYCOPODIOPSIDACEAE
Genus CYCLODENDRON Kräusel, 1928

Type species. C. leslii (Seward, 1903).

Diagnosis. Arborescent lycopod; stems covered with oval leaf scars or laminar leaves borne in a low angle spiral; branching occasional and dichotomous; heterosporous with unisexual subterminal fertile zones.

EXPLANATION OF PLATE 11

Figs. 1–9. *Cyclodendron leslii* (Seward, 1903). 1, BP/2/13456, dichotomously branched axis with spirally arranged leaf scars; there is a small zone of larger scars towards the base of the axis, × 1. 2, BP/2/13315, broad leafless striated axis, × 0·8. 3, BP/2/1327*a*, details of leaf scar on a broad striated leafless axis; the oval scar is flanked by diamond-shaped impressions with a central longitudinal depression, × 9. 4, BP/2/13456, leaf scars; arrow indicates small, presumably vascular pit on the umbo, × 7. 5, BP/2/13256, terminal leafy axis, × 0·5. 6, BP/2/13232, leafless curved axis with narrow central strand (arrowed), × 1·1. 7, BP/2/13457, terminal axis; the large rounded apex is shrouded by a crown of microphylls, × 1. 8, HKS/1, surface of compressed axis showing details of elongate to isodiametric epidermal cells; arrows indicate depressions surrounded by a group of six or seven epidermal cells, SEM micrograph, × 50. 9, BP/2/13462, two groups of microphylls, probably borne on terminal axes, compressed into a fan-shaped pattern; median vascular strand of leaf arrowed, × 0·5.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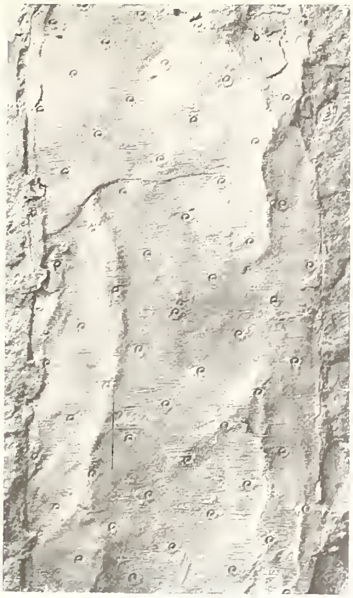
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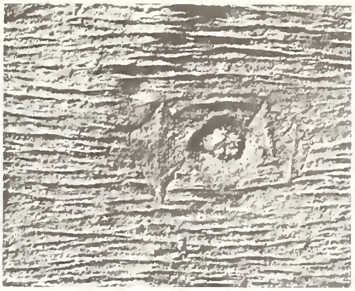
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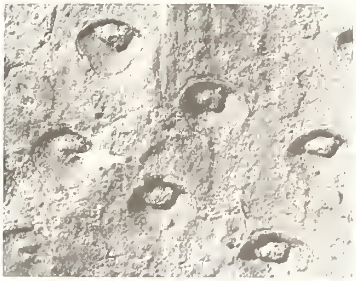
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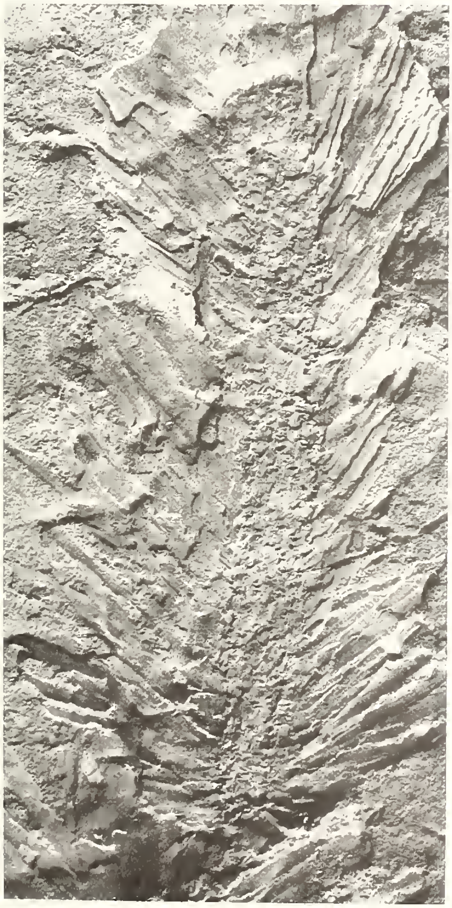
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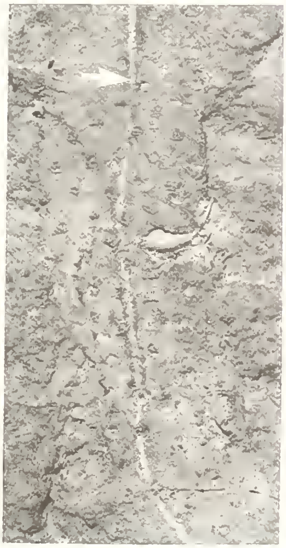
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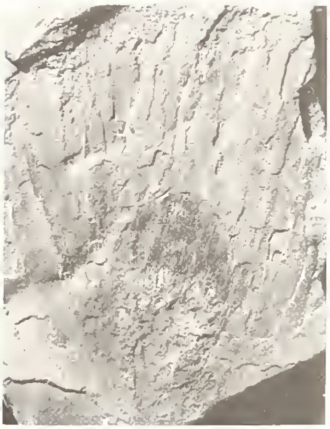
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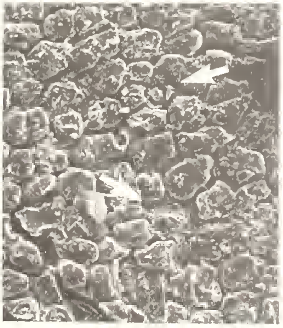
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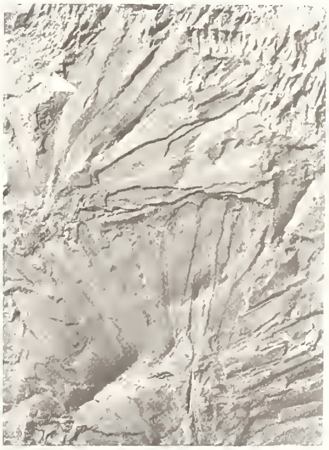
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RAYNER, *Cyclodendron*

Cyclodendron leslii (Seward, 1903)

Plates 11–13; text-fig. 1

Synonymy. See Kräusel (1961).

Holotype. South African Museum 13691 (Seward 1903, pl. 11, fig. 1).

Emended diagnosis. Axes 8 mm–8 cm wide, covered with leaves (axes < 2 cm) or leaf abscission scars (axes > 2 cm); microphylls 3–4 mm wide, up to 8 cm long, with pointed apex and single undivided vascular strand; sunken oval leaf scars containing an umbo just above the centre with small round vascular pit; epidermal cells slightly elongate to isodiametric, 33–120 μm long by 21–45 μm wide; stomata consisting of a central slit-like pore encircled by two narrow guard cells, with cuticle extending into the pore and around the guard cells; stomata (pore and guard cells) 30–60 μm long, 15–27 μm wide; heterosporous with unisexual subterminal fertile zones, microsporangia 3 mm in diameter; megasporangia 1 cm in diameter, containing a single tetrad of megaspores up to 6 mm in diameter; zones of microsporophylls and megasporophylls borne directly on the main axis.

Description. Axes are assigned to *C. leslii* on the distinctive morphology of leaf scars, leaves (where present), and details of the epidermis (cuticle and epidermal cell impressions). There is a danger of misinterpreting surface topography of axes: casts faithfully represent the original surface features, whereas impressions show the reverse. Axes vary in width from 8 mm to over 8 cm. The most conspicuous features of vegetative axes are leaf abscission scars on all parts devoid of leaves (Pl. 11, figs. 1, 2). The scars are oval in outline, widely spaced, and arranged in a low angled spiral with ten to fourteen per gyre. Each scar consists of an oval depression with a raised portion (umbo) just above the centre (Pl. 11, fig. 4). The umbo on a few examples has a small round central pit (Pl. 11, fig. 4, arrowed), presumed to be the site of the vascular trace. There is no leaf cushion. Leaf scars on some wide axes are frequently flanked by indistinct, diamond-shaped areas (Pl. 11, fig. 3) which may be parichnos scars. The wider axes also commonly have a striated appearance (Pl. 11, figs. 2, 3) produced by small transverse ridges.

A narrow ribbon-like strand is preserved in several specimens. The strand is up to 2 mm wide and is either centrally placed or follows a sinuous path through the cortical region (Pl. 11, fig. 6, arrowed); I interpret the strand as xylem. Since several narrow axes are curved (Pl. 12, fig. 3; Pl. 13, fig. 5), it seems possible that they were pliable, rather than rigid, and more prone to twisting during post-mortem transport and burial. However, I consider *Cyclodendron* to have been arborescent and the tips of some terminal axes may have originally been recurved and pendulous, as in many arborescent lycopods.

All axes wider than 2 cm are leafless, and their leaf scars are therefore evidence for abscission. Narrower specimens are commonly covered with leaves. One axis, just 2 cm wide, has a few leaves still attached (Pl. 12, fig. 3). One specimen shows details of a terminal axis (Pl. 11, fig. 7): the apex is rounded, just over 1 cm wide, and shrouded in leaves. Of the several hundred specimens examined, branching was only observed in three specimens; in each, divisions are dichotomous (Pl. 11, fig. 1). Branching axes are about 1·5 cm wide.

The leaves are laminate with approximately parallel edges that taper abruptly to a point at the apex (Pl. 13, fig. 2). They are up to 8 cm long and 3–4 mm wide, and so numerous on terminal axes that they are compressed

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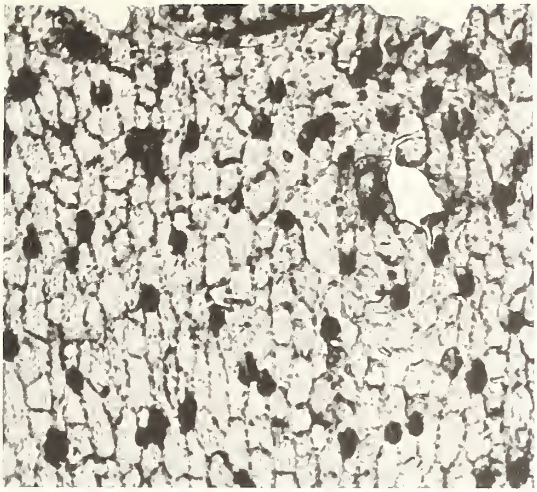
EXPLANATION OF PLATE 12

Figs. 1–7. *Cyclodendron leslii* (Seward, 1903). 1, HK/34, cuticle with reticulum of epidermal cell impressions; black spots correspond to stomata, × 85. 2, HKS/2, internal surface of cuticle showing cell flanges, × 80. 3, BP/2/13455, bent, partially leafy axis showing variation in size of leaf scars; larger scars appear closer together (arrowed) and may correspond to attachment points of sporophylls, × 0·5. 4, HKS/2, stoma showing upstanding flanges believed to be an extension of cuticle down into pore and over guard cells, × 1000. 5, HK/34, indistinct epidermal cell flanges around stoma consisting of thickened cuticle with oval outline and central elongate pore (dark line), × 1000. 6, HK/34, cuticle with rounded internal thickening showing annular gap and associated cracks, × 500. 7, HK/34, internal cuticular thickening; margin extends between adjacent epidermal cells, × 600.

1, 5–7, light micrographs; 2, 4, SEM micrographs.



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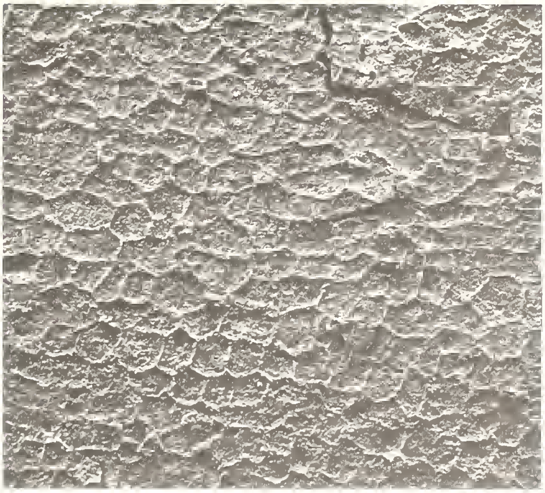

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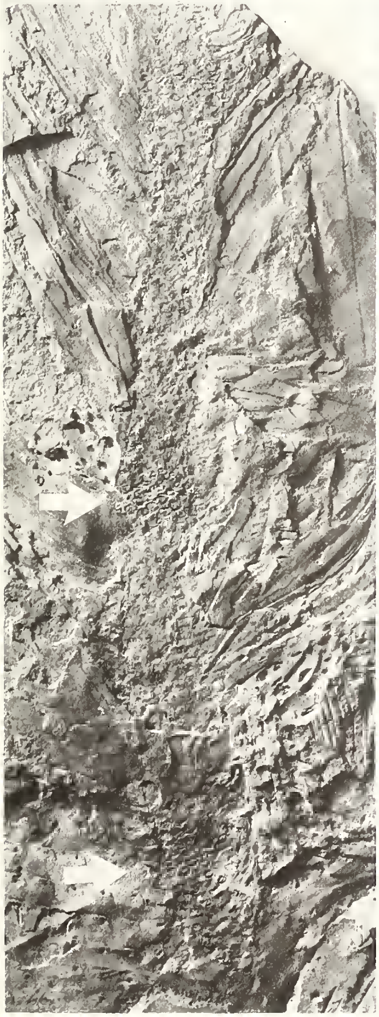

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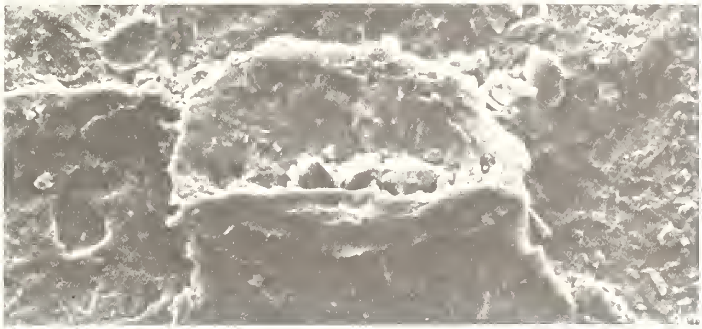

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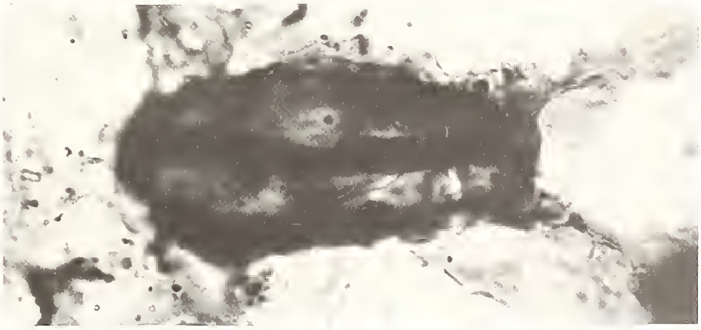

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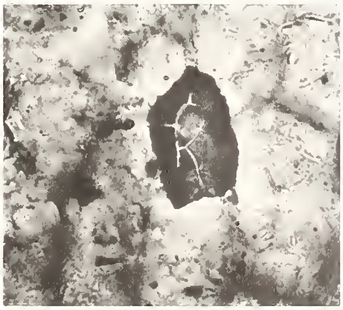

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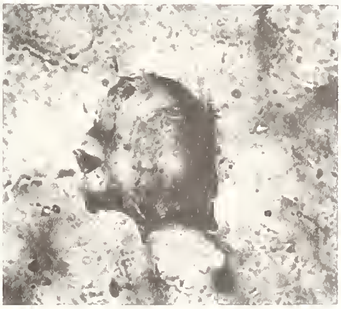


7

RAYNER, *Cyclodendron*

into fan shapes (Pl. 11, figs. 5, 7, 9). Each leaf has a single, undivided, median vascular strand (Pl. 11, fig. 9, arrowed). The surface of the leaf impression is smooth, in contrast to the cellular topography of the axes.

So fine is the matrix at Vereeniging that outlines of individual epidermal cells have been preserved (Pl. 11, fig. 8), identical in shape and size to the cellular pattern preserved on the inner surface of cuticle from Hammanskraal (Pl. 12, fig. 2). The cells are slightly elongate to isodiametric; elongation is either parallel to the long axis of the stem, or in a radiating pattern around scars. Interrupting the general pattern are small groups of six or seven cells which surround a depression that is itself about the size of one cell (Pl. 11, fig. 8, arrowed). These depressions are probably stomata.

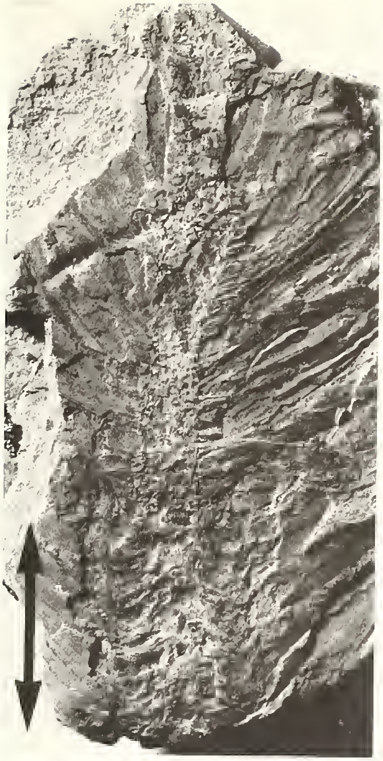
Cuticle was removed from coalified compressions in the areas between leaf scars, there being no evidence of cuticle over the scars themselves. The epidermal cell impressions are delimited by cuticular flanges shown as dark lines on light micrographs (Pl. 12, fig. 1), and upstanding ridges on scanning electron micrographs of the cuticle's inner surface (Pl. 12, fig. 2). The cells are 33–120 μm long and 21–45 μm wide ($\bar{x} = 68 \times 30$ μm, 180 measurements). In addition to the epidermal cell impressions there are numerous, small, circular to lens-shaped dark areas (Pl. 12, fig. 1) which correspond to thickenings on the inner surface of the cuticle (Pl. 12, fig. 4). The lens-shaped or oval thickenings often have a longitudinal slit-like pore in their centre (Pl. 12, fig. 5), resembling a stoma. Some of the circular thickenings, however, have an annular gap in the form of either a complete or incomplete ring (Pl. 12, fig. 6); occasional examples have a radiating pattern of cracks. I interpret this ring with associated cracks to be the result of damage during compression. Also, the circular thickening in a few examples extends between adjacent epidermal cells (Pl. 12, fig. 7). I regard the lens-shaped areas with pores as stomata and suggest that cuticle originally extended down into the pore and around the guard cells. The circular areas with no evidence of pores may possibly represent trichome bases, but no hairs were found attached; I think it unlikely that such internal thickenings would be associated with trichome bases, and more probable that they also represent stomata. Assuming all the dark areas to be stomata, the stomatal index varies between twelve and sixteen. The stomatal apparatus thus consists of a slit-like pore encircled by two elongate guard cells (Pl. 12, fig. 5) which are considerably narrower than the surrounding epidermal cells. The stomatal apparatus (pore and guard cells) is 30–60 μm long and 15–27 μm wide (ninety-nine measurements). Plate 12, fig. 4 shows an internal flange which I regard as cuticle extending down into the pore and which probably covered the underside of the guard cells. The inner thickening was formed by compression during fossilization (text-fig. 1D–F).

Several axes bearing both microsporangiate and megasporangiate zones have been found. The axes are all leafy and 1·0–1·5 cm wide (Pl. 13, fig. 1); I regard them as fertile from the evidence of impression fossils alone. The microsporangiate zones are subterminal in position and are identified by the modified sporophylls. These leaves differ from the others, being recurved close to the point of attachment, and they occur in discrete zones (Pl. 13, figs. 1, 4). Microsporangia are apparently borne singly and are small (up to 3 mm diameter) rounded bodies preserved mostly on the axes. A few examples occur in association with sporophylls (Pl. 13, fig. 4, arrowed). Each microsporangium was held in a cup-like structure formed by the curve in the sporophyll (text-fig. 1B, C). Repeated attempts to obtain *in situ* microspores failed and no dispersed spores were recovered from macerating fragments of the sediment. Evidently, all organic matter has been removed.

Megasporangia are preserved in clusters, on or close to axes (Pl. 13, fig. 3). Preservation is poor, yet Plate 13, fig. 3 shows five megasporangia, each on a sporophyll, close to the point of attachment. Each megasporangium is circular to subtriangular in outline, up to 1 cm in diameter, and appears to contain a single tetrad of large spores (Pl. 13, fig. 6). Each megaspore may be up to 6 mm in diameter. Plate 13, fig. 6 shows a triradiate megaspore (arrowed) in a group of three, presumably part of a tetrad. Plate 12, fig. 3 shows a zone of leaf scars of different sizes which may be related to the position of sporophylls. The presence of leaves on this possibly fertile axis suggests that sporangia may have been abscissed with the sporophylls.

EXPLANATION OF PLATE 13

Figs. 1–6. *Cyclodendron leslii* (Seward, 1903). 1, BP/2/13461, terminal leafy axis with microsporangiate zone in subterminal position (double arrow marks extent of fertile zone); sporophylls are curved close to their point of attachment, ×0·6. 2, BP/2/13287, probable microsporangiate zone with well-preserved leaf impressions, ×0·8. 3, BP/2/13257*a*, five megasporangia associated with sporophylls, ×0·9. 4, BP/2/13460, leafy microsporangiate axis with straight microphylls above zone of recurved sporophylls; arrows indicate position of two microsporangia, ×0·5. 5, BP/2/13454, bent, leafless branching axis with central vascular strand (arrowed); axis shows variation in frequency of scars, ×0·4. 6, BP/2/13459, subrounded megasporangium showing three spores of presumed tetrad; arrow indicates triradiate mark, ×4.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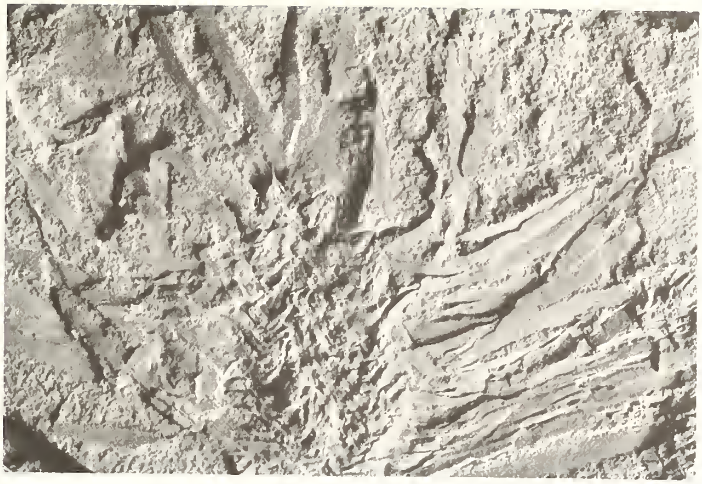
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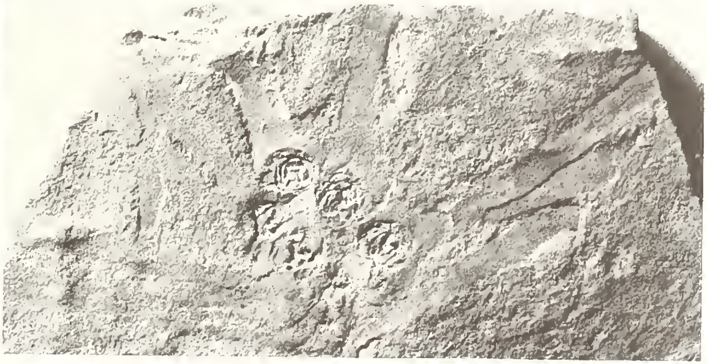
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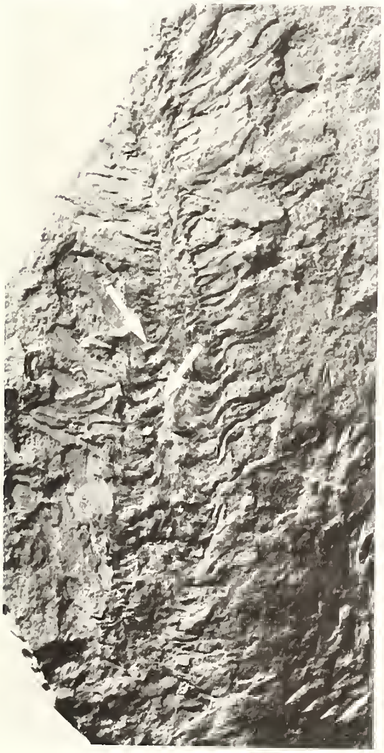
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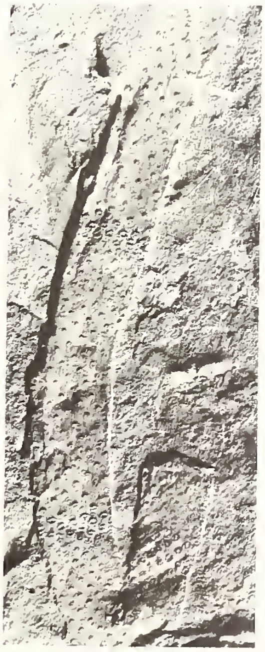
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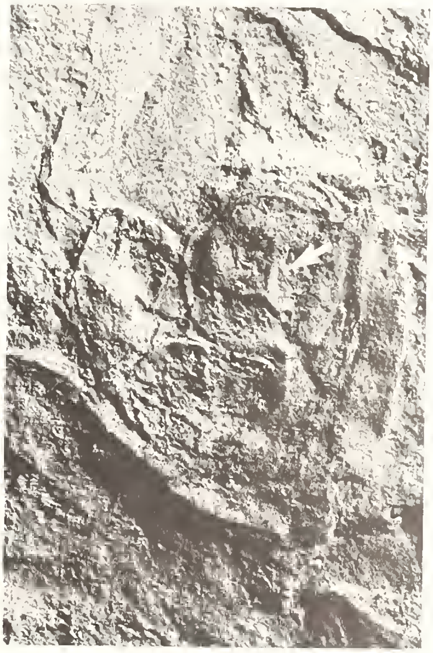
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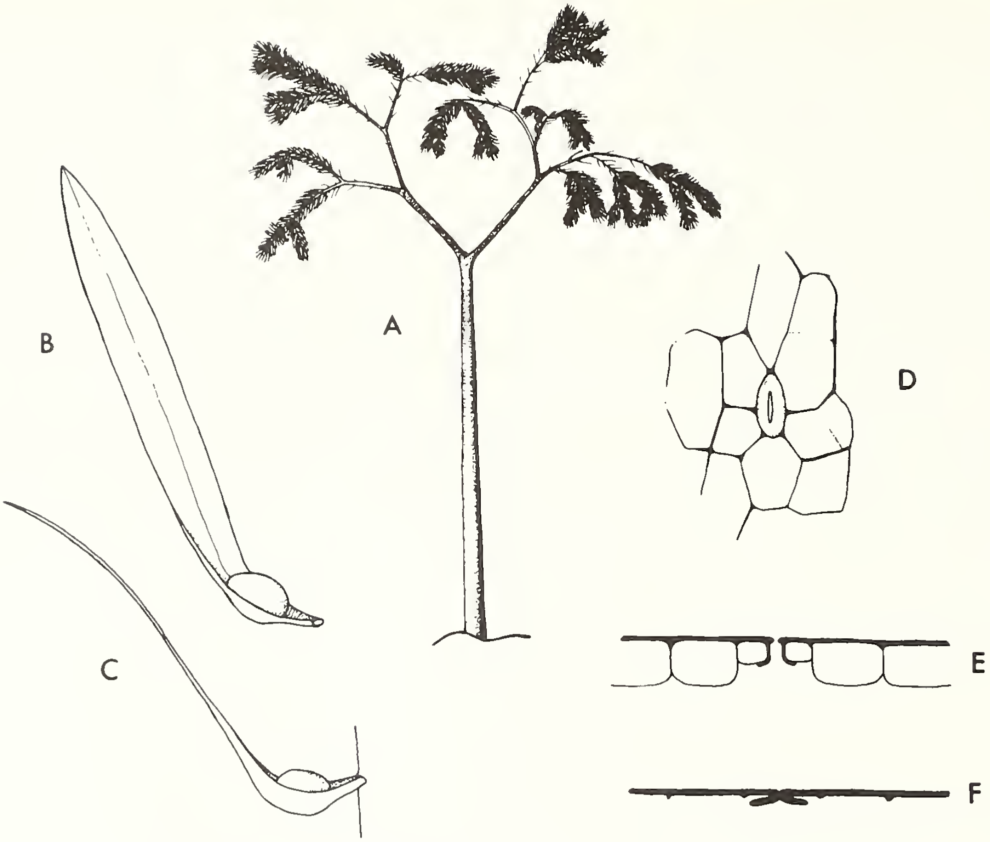
RAYNER, *Cyclodendron*



TEXT-FIG. 1. Reconstructions of *Cyclodendron leslii* (Seward, 1903). A, speculative reconstruction showing arborescent growth habit, occasional dichotomous branching, and leafy terminal axes (some bearing subterminal fertile zones). B, oblique view and C, side view of microsporangiate sporophyll, actual size; the sporangium probably sat in a cup formed by a bend in the sporophyll. D, fossil stoma consisting of elongate pore encircled by thickened cuticle and surrounded by epidermal cell impressions, ×200. E, transverse section of stoma showing original arrangement of cuticle extending down into pore around guard cells. F, cuticle in E after fossilization; cuticle that extended into pore has been compressed, forming two internal flanges (cf. Pl. 13, fig. 3).

Discussion. Three genera of southern hemisphere Permian lycopods have been reported: *Cyclodendron* Kräusel, 1928, *Lycopodiopsis* Renault, 1890, and *Lycopodiophloios* Kräusel, 1961. Sommer and Trindade (1966) reviewed *Lycopodiopsis* and *Lycopodiophloios* and indicated that they are the only genera so far known from the Brazilian Gondwana, suggesting also that both genera were heterosporous. In his review of the lycopods, Chaloner (1967) placed all three southern hemisphere Permian genera in the Lycopodiopsidaceae. The defining characteristics of the family are: an absence of leaf cushions and, where fertile axes are known, sporophylls inserted directly on the main axis. Chaloner (1967) reproduced Seward's (1903) and Kräusel's (1961) illustrations; he also figured a specimen (1967, fig. 355) with closely spaced, diamond-shaped leaf scars which is clearly unlike all other specimens described as *Cyclodendron* and must be discounted as its affinities lie elsewhere.

Lycopodiopsis was described by Renault (1890) for permineralized vegetative axes. These axes, now called *Brasilodendron* Chaloner *et al.*, 1979, have typically closely spaced, diamond-shaped leaf scars and occasionally narrow leaves. These features alone contrast sufficiently with *Cyclodendron*, but the new fertile material and axes with cuticle described here reinforce the separation of the two genera.

Kräusel (1961) erected the genus *Lycopodiophloios* for broad vegetative axes from Vereeniging. He interpreted some narrow leaves scattered in the matrix as having an organic connection to the axes. These axes have leaf scars identical to those of *Cyclodendron*. Kräusel regarded the striated surface of the axes and the diamond-shaped impressions flanking the leaf scars as sufficiently different from known *Cyclodendron* axes to require a new genus. In the absence of fertile axes of *Lycopodiophloios*, I think it unjustified to erect a new genus; I unite the sterile *Lycopodiophloios* axes with *Cyclodendron* on the basis of their epidermal features (identical size, shape, orientation of cells, and arrangement of stomata) and leaf scars (identical size, shape, arrangement in a low angled spiral, with ten to fourteen scars per gyre). I suggest that the diamond-shaped impressions associated with the scars and striations on broad axes (Kräusel's *Lycopodiophloios* and my Pl. 11, fig. 8), but absent on narrow axes, were features only of main stems which had reached a certain size. Kräusel reported no small, presumably juvenile, *Lycopodiophloios* axes whereas I have found all sizes of *Cyclodendron* from 8 mm to 8 cm. I believe that Kräusel's leafy specimen (1961, fig. 48) results from fortuitous accumulations of leaves close to the axis. Unfortunately, the two types of axis (i.e. the narrow *Cyclodendron* and the broad *Lycopodiophloios*) are unlikely to be found connected unless an almost complete specimen is discovered. I doubt also whether fertile *Lycopodiophloios* axes will ever be found since I interpret them as main stems which would not have carried sporangia. Rather than leave *Lycopodiophloios* as a permanent form genus, I unite these broad axes with *C. leslii*.

Cyclodendron contrasts with the two Carboniferous herbaceous genera from Argentina, *Bumbodendron* and *Malanzania* Archangelsky *et al*., 1981. *Bumbodendron* is characterized by closely spaced fusiform leaf cushions, and *Malanzania* by false leaf scars and small spiny leaves. The resemblance of *Cyclodendron* to *Bothrodendron*, first noticed by Seward (1903), is superficial. *Bothrodendron* is a Carboniferous genus with small ligulate leaves and definite terminal cones, while *Cyclodendron* is apparently eligulate with large leaves and subterminal fertile zones. Similarly, *Caenodendron* Zalessky, 1918 from the lower Carboniferous has only superficially similar leaf scars.

The size of vegetative axes, up to 8 cm wide, suggests an arborescent habit for *C. leslii* (text-fig. 1A). Arborescent lycopods were uncommon after the Carboniferous, becoming extinct at the end of the lower Permian (Chaloner 1967). Kräusel (1961, figs. 32, 36–38) figured a single specimen which he considered fertile; he identified both megasporangia and microsporangia on the axis but I can see evidence only for megasporangia. This single fertile zone is on an impression fossil from Vereeniging (no *in situ* spores were recovered) and, since I have found several fertile axes which support either microsporangia or megasporangia but never both, I interpret *Cyclodendron* as having unisexual fertile zones. The presence of fertile zones rather than cones is a common feature in lower Carboniferous lycopods world-wide (Archangelsky *et al*. 1981). This type of organization persisted into the upper Carboniferous and, in the case of *Cyclodendron*, into the lower Permian of the Gondwana realm.

Du Toit (1932, p. 405) first stressed the importance of *C. leslii* as a potential index fossil, ranging from the 'Middle Ecca (Union) to the lowest Beaufort Beds (Wankie) and hence typically lower Permian'. *C. leslii* has also been reported from sediments of the same age in India (Maithy 1965). The extensive collections at the Bernard Price Institute support *C. leslii* as a lower Permian index fossil, with no evidence of the distinctive axes from younger sediments.

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FLUID TRANSPORT PROPERTIES OF *NAUTILUS* SIPHUNCULAR TUBE: WITHIN-CAMERA DISTRIBUTION OF FLOW RATE

by JOHN A. CHAMBERLAIN JR. *and* STEPHEN W. PILLSBURY

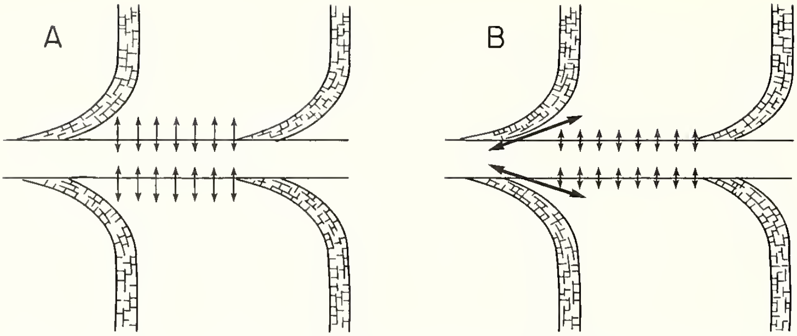
Abstract. There are two viewpoints concerning the nature of flow across the siphuncular tube of *Nautilus* and other ectocochliates: (1) flow is uniform along the length of the tube; (2) flow is mainly localized in the septal necks. We tested these alternatives in specimens of *N. pompilius* by measuring flow rates through septal necks sealed with epoxy. We found that the septal neck, and specifically the so-called pillar zone, is not a conduit for fluid transport. Fluid entering or exiting the camerae flows uniformly through the permeable conchiolinous membranes of the connecting ring. This situation is the result of two factors: (1) the connecting ring is provided with osmotically active epithelial cells whereas the septal necks are not; and (2) the pillar zone is not porous, but consists of a solid array of crystal matrix intergrowths. The actual function of the pillar zone appears to lie in the direction of optimizing the mechanical strength of the septum-connecting ring junction and of minimizing the metabolic cost of constructing the connecting ring. The microstructure of the septal neck in many fossil cephalopods is consistent with this interpretation. Evaluation of siphuncle function and adaptation in fossil forms, and of evolution in siphuncular structure, must take account of the fluid transport properties of the connecting ring.

Buoyancy control in *Nautilus* occurs by a process of local osmosis initiated by the epithelial cells lining the inner side of the siphuncular tube (Denton and Gilpin-Brown 1966, 1973; Denton 1971, 1974; Greenwald *et al.* 1980; Ward 1980; Greenwald *et al.* 1982). Fluid flows into or out of the camerae in response to the relative osmolarity of the water reservoirs on opposite sides of the siphuncular tube (cameral water and intracellular fluid respectively). Since fluid must pass through the wall of the siphuncular tube, fluid transport properties of the tube are of paramount importance in buoyancy regulation. Collins and Minton (1967) Chamberlain (1978), and Chamberlain and Moore (1982) have examined tube transport by introducing water under high hydrostatic pressure into the siphuncular tubes of freshly killed animals. Measurement of the passive flow thus induced suggests that the permeability coefficient of the tube is very low ($\sim 2{\cdot}4 \times 10^1\ \mu$d; Chamberlain 1978), but that this is sufficient to provide flow rates up to about three orders of magnitude greater than the rates of osmotic flow actually observed in live animals (Chamberlain and Moore 1982). The transport capacity of the tube apparently provides no significant impediment to fluid movements necessary for buoyancy control.

Implicit in this experimental work on osmotic flow and tube transport has been the view that within a chamber, fluid movement is roughly uniform along the length of the tube. No specific portion of the siphuncular tube has been recognized in these efforts as accounting for the bulk of fluid transport (text-fig. 1A). This notion has recently been challenged by Bandel and Boletzky (1979), who assert that fluid transport is centred primarily near the contact between the septal neck and siphuncular tube (text-fig. 1B). According to these authors, pillar-like structures lining the adapertural surface of the nacreous layer in the septum continue into the septal neck (text-fig. 2). On the basis of its apparently open, portico-like structure, Bandel and Boletzky identify this pillar zone of the septal neck as being highly porous, much more so than the conchiolinous horny tube, and suggest therefore that the pillar zone must be the primary conduit for fluid transport across the siphuncle.

The pillar zone theory has been amplified by the discovery (Obata *et al.* 1980; Bandel 1981; Tanabe *et al.* 1982) that pillar zones seem to occur in a variety of fossil ectocochliates as well as in *Nautilus*.

[Palaeontology, Vol. 28, Part 1, 1985, pp. 121–131.]

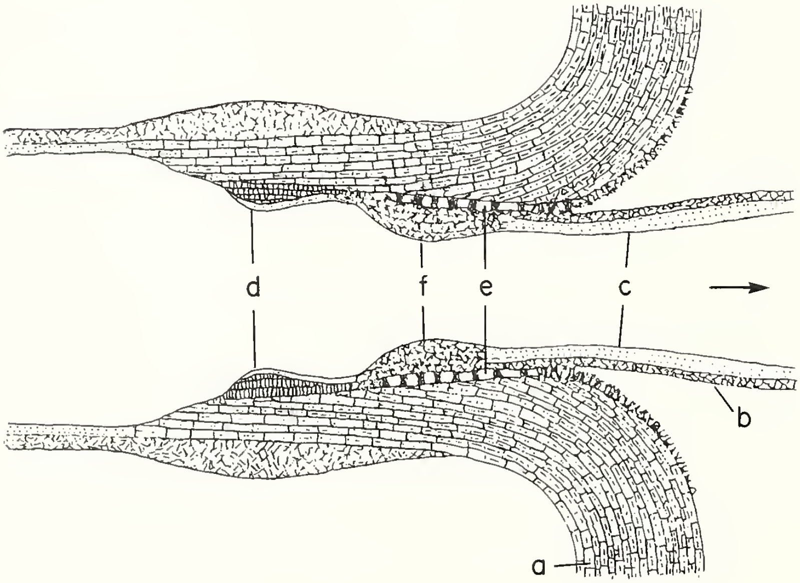


TEXT-FIG. 1. Contrasting models of relative flow rates across siphuncular tube. Arrow lengths indicate approximate magnitude of flow at specific sites along tube. A, uniform flow theory. B, localized pillar zone flow theory of Bandel and Boletzky (1979).

Further support is given to Bandel and Boletzky's claim by the presence of pillar zones through which fluid undoubtedly flows in sepiid cuttlebone and in the siphuncle of *Spirula* (see Bandel and Boletzky 1979).

PALAEOBIOLOGICAL IMPLICATIONS OF PILLAR ZONE FLOW

The question of whether fluid transport occurs uniformly along the siphuncular tube or preferentially through the pillar zones is one of considerable importance in interpreting the functioning of the ectocochliate buoyancy mechanism. In particular, comparisons of siphuncular microstructure, as represented in Palaeozoic nautiloids and *Nautilus* (Mutvei 1972*a*, *b*) or among nautiloids and ammonoids (Birkelund and Hansen 1968, 1974; Mutvei 1972*a*, *b*; Kulicki 1979; Obata *et al.* 1980; Bandel 1981; Tanabe *et al.* 1982), will of necessity take on different meanings according to the weight assigned to the two opposing views of fluid transport. Most importantly, analysis of the adaptive significance of the varied septal neck geometries seen in fossil cephalopods, or of connecting ring structures, as observed for instance in the Devonian nautiloid *Archicoceras* (Crick and Teichert 1979), would lead to radically different viewpoints depending on how one interprets the presence or absence of pillar zones and their role in cephalopod buoyancy. If pillar zone flow of the kind



TEXT-FIG. 2. Longitudinal section through siphuncular tube and septal neck of *Nautilus pompilius* (after Bandel and Boletzky 1979, fig. 21). *a*, septal nacre; *b*, chalky layer; *c*, horny layer; *d*, inner ridge; *e*, pillar zone; *f*, spongy region.

advocated by Bandel and Boletzky actually occurs, then connecting ring permeability and geometry become meaningless flow transport parameters because fluid movement, being centred in the septal necks, would largely bypass the rest of the siphuncular tube. If we accept the pillar zone model, we must reject the analyses of siphuncle functional morphology provided by Denton and Gilpin-Brown (1966), Collins and Minton (1967), Chamberlain (1978), Chamberlain and Moore (1982), and Ward (1982).

AIM OF THIS WORK

The question of siphuncle flow localization raised by Bandel and Boletzky (1979) is clearly a significant one for ectocochliate biology. Yet, in the five years since their paper has appeared no effort has been made to substantiate the position advocated in it through analysis of tube flow properties. The growing acceptance of the localized flow theory among some cephalopod specialists is based only on intuition concerning the apparent porous nature of the pillar zone, and on uncertain analogy with siphuncle function in endocochliates. In this paper we report results of an experiment dealing with hydrostatically induced flow through open and sealed septal necks of *N. pompilius*. It is our purpose to provide data that will help discriminate between these contrasting alternatives.

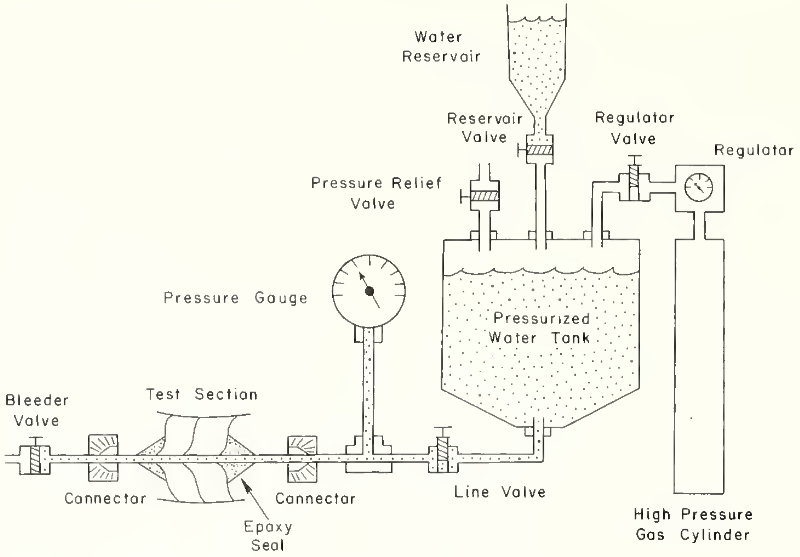
MATERIALS AND METHODS

Our testing procedure is based on that devised by Chamberlain and Moore (1982) for measuring siphuncular flow rate in *Nautilus* shells. Two fresh shells, described in Table 1, were sectioned about 1 cm from the mid-plane to reveal the siphuncle. Using forceps, we extracted the siphuncular tissue from the tube and then attached a ten to fifteen chamber length of tube, still wet, undecayed, and intact in the shell, to our testing apparatus. This consists of three main components (text-fig. 3): (1) a pressurized gas cylinder and regulator for inducing high fluid pressure in the test system; (2) a water reservoir for converting gas pressure to hydrostatic pressure; and (3) instrumentation for reading the pressure of the water in the siphuncular tube. A specimen is connected to the apparatus by inserting a high pressure line from the pressure gauge a short distance into the open septal neck of the outermost septum of the section to be tested, and cementing it in place with epoxy resin. The system is pressurized by releasing gas into the water reservoir. This elevates the hydrostatic pressure in the test section and causes water to flow outward across the permeable wall of the siphuncular tube. Water thus expelled from the siphuncle collects in the camerae from which it is then withdrawn and its volume determined by pipette. Chamberlain and Moore (1982) fully describe the apparatus and basic testing procedure.

TABLE 1. Data for specimens tested in this paper. Test interval = length of time between death of animal and testing.

Specimen	Shell weight (gm)	Shell diameter (cm)	Total number of chambers	Test interval (days)
A	246	11·8	36	2
B	109	8·5	28	0

Our method for identifying the contribution of the pillar zone to overall siphuncular flow consisted of two steps. First, we determined flow rate through fresh tubes prepared only as described above, i.e. with tissue removed. In both specimens listed in Table 1, flow in each chamber of the test section was measured at a variety of pressures from about 10 to 40 bars. Because this testing configuration involves an unaltered tube wall, observed flow rates will reflect the full contribution of pillar zone flow. When unaltered flow rates had been determined in this way, we modified the septal necks in order to interfere with flow through the pillar zone. This was done by mechanically removing the pellicle and chalky layer from the connecting ring and septal neck,

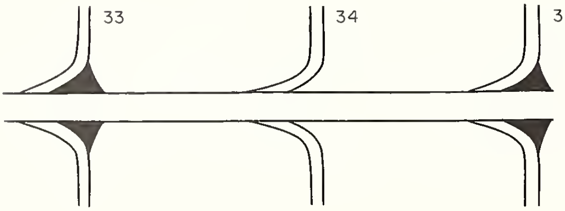

Water Reservoir
Reservoir Valve
Regulator Valve
Regulator
Pressure Relief Valve
Pressure Gauge
Pressurized Water Tank
Bleeder Valve
Test Section
Connector
Connector
Epoxy Seal
Line Valve
High Pressure Gas Cylinder

TEXT-FIG. 3. Testing apparatus for measuring flow across wall of the siphuncular tube (after Chamberlain and Moore 1982, fig. 1).

and covering the area thus exposed with epoxy. To ensure a watertight seal over the pillar zone, we used a specialized resin called Aquatapoxy, manufactured by the American Chemical Co., Palo Alto, California, which is formulated to adhere to wet surfaces. As indicated in Table 2, we sealed an alternate series of septal necks in the test sections of our two specimens. Text-fig. 4 shows the appearance of a portion of the test section in specimen A after preparation with epoxy. The unaltered necks in these sequences were used for experimental control. After preparation was complete, the sealed-unsealed sequences were tested as described above. Fluid passing through the siphuncular tube was again collected in the camerae and measured. Since the pillar zones in alternate, sealed necks could not now transport water, comparing the volume of water passing through such test segments to the flow through unaltered necks revealed the relative importance of pillar zone flow to overall flow of fluid across the siphuncular tube.

TABLE 2. Sequences of septal necks examined in the two specimens studied here. S—septal necks sealed with epoxy. O—septal necks open (unsealed). Septa identified by sequence number as counted from apex of shell.

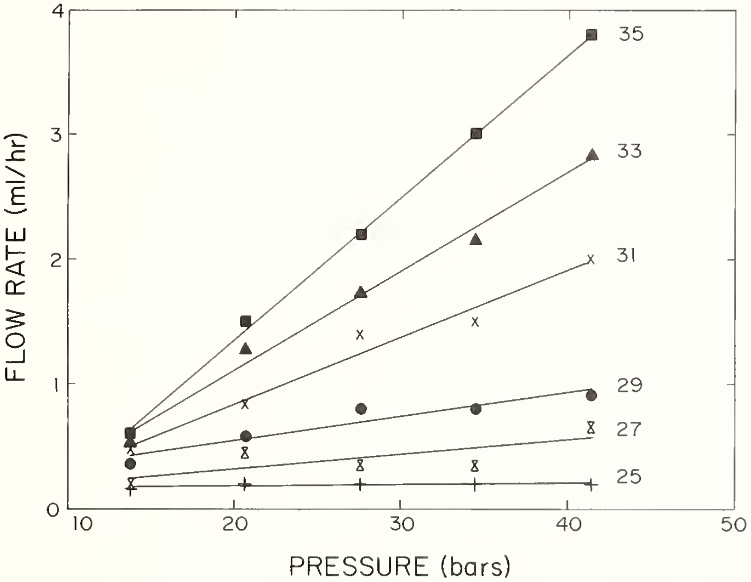
Specimen A	S	35		33		31		29		27		25
	O		34		32		30		28		26	
Specimen B	S	26		24								
	O		25		23							



TEXT-FIG. 4. Test configuration for a portion of specimen A after alternate septal necks (35 and 33) had been sealed with epoxy. Septa numbered in ascending order from shell apex.

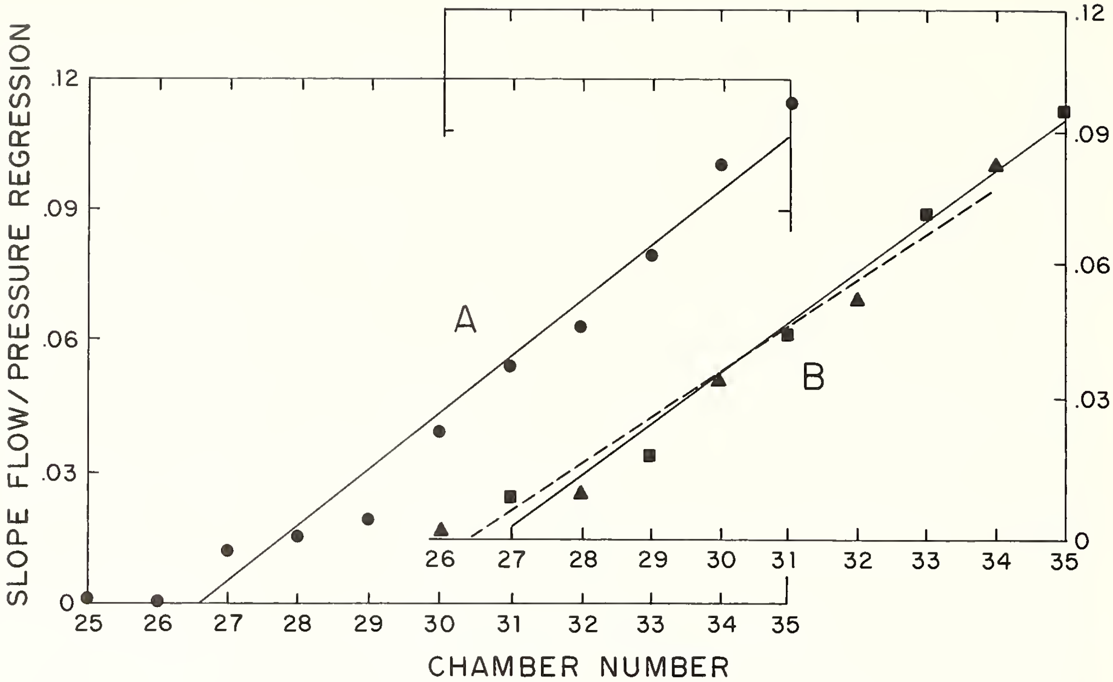
FLOW RATES IN UNALTERED NECKS

Text-fig. 5 shows the relationship between volumetric flow rate and different values of applied pressure for the segment of siphuncular tube in each of six chambers in specimen A. These results apply to the initial series of runs in which none of the septal necks in the test series had been sealed with epoxy. Data for even-numbered chambers in the sequence fall in the appropriate positions between adjacent odd-numbered chambers but have been omitted for clarity. The second specimen yielded similar results.



TEXT-FIG. 5. Siphuncular flow rate plotted as a function of hydrostatic pressure for six chambers in specimen A. Data for unaltered septal necks. Scatter for each chamber fitted with linear regression. Chamber number at right-hand end of each regression line.

Several features of text-fig. 5 are worth noting. First, measured flow rates (~0·5–4·0 ml/hr) are about the same as rates previously obtained for *N. pompilius* (Chamberlain and Moore 1982), and are much higher than osmotic pumping rates in live animals, as these authors point out. Increasing hydrostatic pressure induces higher flow rates in all of the siphuncular segments studied. Flow rate increases linearly with pressure. Note also that tube segments in the volumetrically larger chambers (i.e. those with higher sequence numbers) exhibit higher slopes than earlier formed, smaller chambers. This pattern is seen in the data for all shells so far tested (see Chamberlain and Moore 1982), and would thus appear to respresent the response of normal siphuncular tubes to elevated pressure. The overall behaviour of the test section can be illustrated by plotting the slopes of the curves in text-fig. 5 as a function of the position of each chamber in the sequence of chambers composing the phragmocone. This is done in text-fig. 6A. A simple, linear relation in these parameters is evident over the range of chambers represented in the test section. We would point out that this relation cannot, however, hold over the entire phragmocene because chambers formed early in the sequence cannot vary in slope significantly from chambers 25–26. The relationship for the whole phragmocone is probably some sort of power function similar in form to the relationship between siphuncle surface area and chamber sequence number observed by Chamberlain and Moore (1982) and Ward (1982).

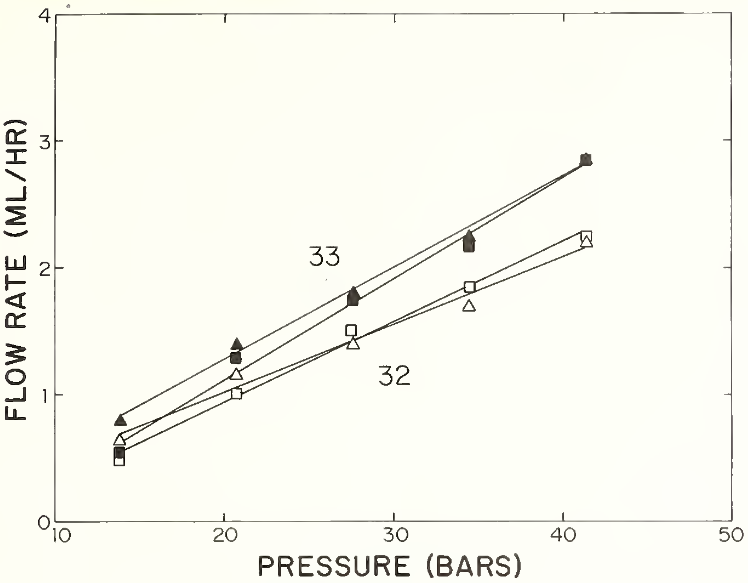


TEXT-FIG. 6. A, slope of flow rate–pressure regressions for tube segment in each chamber of specimen A tested, plotted as a function of chamber sequence number. Chamber number increases toward shell aperture. All septal necks unsealed. B, slope of flow rate–pressure regressions for tube segments in chambers 26–35 of specimen A. Odd numbered septal necks sealed (squares). Even numbered septal necks open (triangles). All data from second test run. Each data set fitted with linear regression as follows: sealed necks (solid line); $y = 0{\cdot}011\,x - 0{\cdot}032$, $r = 0{\cdot}990$; open necks (dashed line); $y = 0{\cdot}010\,x - 0{\cdot}270$, $r = 0{\cdot}985$.

FLOW RATES IN SEALED NECKS

Results obtained for our second series of test runs, in which alternate septal necks (odd numbered ones—see Table 2) were sealed with epoxy, give little evidence of a primary role for the septal necks in cameral fluid transport. Text-fig. 7 shows data for one such sealed neck. Flow rates obtained when septal neck 33 was sealed (solid squares) are little different from flow rates observed when this septal neck was unaltered (solid triangles). Statistical analysis (t-tests) of these two data sets (see Zar 1974, pp. 228–230) are unable to separate either slopes ($p = 0{\cdot}24$) or y-intercepts ($p = 0{\cdot}79$). Within the resolving power of our procedure, the two results are, in effect, identical. Sealing the septal neck with epoxy has no apparent effect on flow. As noted above, if the Bandel and Boletzky flow model were valid, one would expect a significant reduction in flow rate when septal necks are sealed. The absence of such a situation indicates that this model is not correct. Fluid must move across the wall of the siphuncular tube more or less uniformly along its entire length. It is not appreciably localized in the septal necks.

This interpretation is strengthened when we broaden our analysis to include other chambers in the test sequence. Text-fig. 7 also shows data for an adjacent chamber, but one which we left unaltered as a control during both series of tests. Results generated during the first test series (all necks unaltered) are shown as open squares, while data obtained in the second set of runs (odd numbered necks sealed) are indicated by open triangles. In both cases, septal neck 32 remained unsealed, and in both cases the flow data are coincident. Once again, Zar's procedure is unable to discriminate between these data



TEXT-FIG. 7. Flow rate for siphuncular tube segments in chambers 32 and 33 of specimen A. Solid squares—data from initial test series for chamber 33 in which septal neck has not been sealed. Solid triangles-data from second test series for chamber 33 in which septal neck has been sealed with epoxy. Open squares—data from initial test series for chamber 32; septal neck not sealed. Open triangles—data from second test series for chamber 32; septal neck not sealed. Each data set fitted with linear regression as follows: chamber 33 (unsealed neck), $y = 0{\cdot}079\ x - 0{\cdot}480$, $r = 0{\cdot}995$; chamber 33 (sealed neck), $y = 0{\cdot}072\ x - 0{\cdot}164$, $r = 0{\cdot}944$; chamber 32 test series 1: $y = 0{\cdot}063\ x - 0{\cdot}330$, $r = 0{\cdot}996$; chamber 32 test series 2: $y = 0{\cdot}053\ x + 0{\cdot}044$, $r = 0{\cdot}991$.

sets ($p = 0{\cdot}11$ and $p = 0{\cdot}98$ for slopes and y-intercepts respectively). These results show that the overlap seen in the sealed-unsealed data for chamber 33 is not likely to have derived from unrecognized variation in test conditions, i.e. this similitude is not a consequence of a major system-wide fluctuation in some test parameter that fortuitously and precisely offsets a real reduction in flow for the sealed neck. If this were to have occurred, the data for chamber 32 would show it as a separation of the data sets for the two test series. The data for other even-numbered chambers (in which septal necks are left unsealed) give the same results.

Our ideas are also strengthened by pooling our data for all sealed septal necks. Table 3 gives these results as well as the outcome of statistical evaluations of their significance. Again, we rely on regression parameters to express the relation between flow rate and applied pressure. In four of the five cases summarized in Table 3, the slopes of the regressions of the open and sealed test configurations cannot be separated at acceptable levels of significance. In all five chambers, the y-intercepts do not differ. Even in the single instance (chamber 35) where the slopes of the open-neck and sealed-neck regression differ at acceptable levels ($p = 0{\cdot}05$), the magnitude of the difference is small in terms of flow rates. For example, at a pressure of 25 bars, about the median of the range tested and a pressure equivalent to the modal depth range of living *Nautilus* populations (Ward and Martin 1980), flow rates for the two test configurations differ by only 16%. This is not the situation envisaged by Bandel and Boletzky (1979) in elucidating their pillar zone model of siphuncular transport.

Arguments about the character of tube transport that we have advanced so far, involve

TABLE 3. Regression parameters for flow rate–pressure data for odd-numbered chambers in specimen 1. Chamber number = chamber sequence number counted adaperturally from shell apen. Septal neck = condition of septal neck during testing: open—septal neck unsealed, pillar zone flow unimpeded; sealed—septal neck sealed, pillar zone flow shut off. Slope = slope of flow rate–pressure regression for test configuration indicated in column 2. *y*-int. = *y*-intercept of flow rate–pressure regression. Slope Comp. = comparison of slopes for open versus sealed data sets using Zar's (1974) procedure: *t*—*t* statistic calculated for regression comparisons; sig.—significance level of *t*. *y*-int. comp. = comparison of *y*-intercepts for open versus sealed data sets using Zar's (1974) procedure. Degrees of freedom: slopes = 6; *y*-intercepts = 7.

				Slope comp.			y-int.comp.	
Chamber no.	Septal neck	Slope	*y*-int.	*r*	*t*	*sig.*	*t*	*sig.*
35	Open	0·114	−0·940	0·999	2·84	0·05	0·598	0·57
	Sealed	0·095	−0·080	0·993				
33	Open	0·079	−0·480	0·995	1·327	0·24	0·275	0·79
	Sealed	0·072	−0·164	0·994				
31	Open	0·054	−0·236	0·986	1·063	0·33	0·057	0·96
	Sealed	0·045	0·029	0·968				
29	Open	0·019	0·156	0·952	0·357	0·73	0·553	0·60
	Sealed	0·018	0·140	0·984				
27	Open	0·012	0·080	0·768	0·543	0·61	0·686	0·52
	Sealed	0·009	0·120	0·968				

comparisons made between different test runs. We can approach this question also by evaluating data from the same test run. Such data are presented in text-fig. 6B, in which we record the slopes of the flow rate–pressure regressions for all chambers tested in our second test series. Odd-numbered chambers contain sealed septal necks, while even-numbered chambers have open, unsealed necks. Note that data for the two different neck configurations fall in the same general area of the graph. In fact, the slopes and *y*-intercepts of the regressions for the sealed necks (solid line) and open necks (dashed line) cannot be separated at acceptable significance levels ($t_{\text{slopes}} = 0{\cdot}752$, $p = 0{\cdot}48$ at d.f. = 6; $t_{y\text{-int}} = 0{\cdot}62$, $p = 0{\cdot}95$ at d.f. = 7). Sealed necks would thus appear to give the same results as open necks. One would not expect this kind of situation to develop if the pillar zones were the primary conduit for fluid transport. Instead, shutting off pillar zone flow by sealing the septal necks should result in a wide disparity between the sealed and unsealed data. The conformity of the data thus argues convincingly against the pillar zone model.

IS CAMERAL FLOW LOCALIZED IN THE PILLAR ZONE?

The data on flow rates for sealed and unsealed septal necks presented in Table 3 and text-figs. 6 and 7, point quite convincingly to the conclusion that the pillar zone, in spite of its apparent high porosity, is not a major passageway for fluid movement across the siphuncular tube. The tenets of Bandel and Boletzky's pillar zone model of fluid transport are not supported by our data. Instead, fluid would appear to move across the connecting rings uniformly.

This result is a most significant one for interpreting the functions of the siphuncle in *Nautilus*. In this regard, we can now see that the statements made by Denton and Gilpin-Brown (1966), Chamberlain (1978), Ward (1982), and Chamberlain and Moore (1982) involving the role of siphuncle geometry and permeability in controlling fluid transport across the tube wall, cannot be rejected (on these grounds at least) as misapprehended. Fluid moves across the tube wall during episodes of osmotic pumping, not through the pillar zones, so that connecting ring permeability, surface area, and other factors identified by these authors must influence this flow in a substantial way. The results we present here indicate that we should put aside such ideas as pillar zone flow and continue to look toward the properties of the siphuncular tube wall, and the tissue that underlies it, for a fuller understanding of the *Nautilus* buoyancy mechanism.

These same considerations apply to fossil cephalopods. Analyses of geometry, material properties, composition, and structural features of connecting rings in fossil forms should be sensitive to the effect of such parameters on cameral flow. Evaluation of siphuncle function, siphuncular adaptation, and evolution of siphuncular structure must take account of fluid transport properties. Our own view is that much of the phylogenetic variation observed in these parameters can be explained in terms of fluid transport and in the status of fluid transport as an important determinant of cephalopod mode of life.

WHAT PREVENTS PILLAR ZONE FLOW?

Passage of fluid through the pillar zone in *Nautilus* is precluded for two reasons. First, the histology of the siphuncular epithelium is not compatible with flow of this type. The septal neck is not underlain by tissue capable of solute-coupled transport (Greenwald, pers. comm. 1984), as would be required in order osmotically to pump fluid directly through the pillar zone. Instead, the connecting ring is associated with such tissue, as is indicated in the sample preparation techniques used by Denton and Gilpin-Brown (1966) and Greenwald *et al.* (1982). The intra-cameral portion of the siphuncular tube is furnished with a pumping mechanism, but the septal neck lacks one. This arrangement is antithetical to the requirements for pillar zone flow.

Secondly, the microarchitecture of the septal neck is not compatible with flow through the pillar zone. In this regard the analyses of Mutvei (1972*b*) and Kulicki and Mutvei (1982) indicate that the spherulitic-prismatic layer of the septal neck (roughly equivalent to Bandel and Boletzky's pillar zone) does not lead directly to the siphuncular epithelium but rather is separated from it by the conchiolinous membranes of the connecting ring. Thus, if fluid could be drawn through the pillar zone (or spherulitic-prismatic region) in the absence of active epithelium, its passage would still be constrained by the fluid conductance properties of the horny tube, just as it would be along the entire length of the connecting ring. Kulicki and Mutvei (1982) show that this is also the case in the ammonite *Quenstedtoceras*. Finally, we also point out that recent studies of siphuncle chemistry (Crick, pers. comm. 1984) involving sample preparation techniques specifically geared toward retaining the non-crystalline components of the shell material indicate that the spaces between the crystal stacks in the pillar zone are not fluid filled as Bandel and Boletzky assert, but are filled by organic matrix. The pillar zone is actually solid, and for this reason cannot convey fluid, or at least, conveys it at a rate constrained by the fluid conductance properties of the conchiolinous matrix.

OF WHAT SIGNIFICANCE IS THE PILLAR ZONE?

If the pillar zone in *Nautilus* does not function as Bandel and Boletzky postulate, what purpose, if any, does it serve? Two possibilities present themselves: (1) the pillar zone may optimize the mechanical strength of the septal neck-connecting ring union; and (2) the pillar zone may be a consequence of unusually rapid carbonate secretion linked to the chamber formation cycle. Several observations are compatible with these hypotheses.

The pillar zone lies along the inner surface of the septal neck (text-fig. 2; see also fig. 1 of Mutvei 1972*a*; and fig. 1 of Kulicki and Mutvei 1982). It therefore occupies a medial position between the crystalline nacreous layer of the septal neck and the conchiolinous membranes of the connecting ring, and as such, must serve as a means of attachment for these two siphuncle components. Conchiolin and nacre diverge widely in their mechanical properties—conchiolin is pliant and elastic, while nacre is rigid and brittle (Wainwright *et al.* 1976). Anchoring such disparate materials firmly enough to resist the severe hydrostatic pressure head encountered at the living depth of *Nautilus* may require the kind of intergrowth of crystalline elements and organic matrix observed by Crick (pers. comm. 1984) in the pillar zone. Thus, the pillar zone may be designed to maximize the strength with which the connecting ring and septal neck are joined. Similar crystal-matrix intergrowths are observed in other examples involving the seating of load-bearing members of different composition, particularly in vertebrate bone and the myostracum of molluscs, in the latter of which carbonate prisms are surrounded by conchiolinous sheaths (Wainwright *et al.* 1976).

Deposition of the pillar zone may also be related to chamber formation. X-ray studies of the chamber formation sequence in live *Nautilus* (Ward *et al.* 1980; Ward and Chamberlain 1983) show that the chamber formation cycle consists of several phases of unequal duration. In this regard, forward movement of the body which occurs in preparation for the secretion of a new septum, requires at the most only about seven days in *N. pompilius* (Ward and Chamberlain 1983). This stage in the chamber formation cycle is a time of rapid secretion of cameral fluid which fills the expanding space between the forward-moving body and the last formed septum. Carbonate and conchiolin, needed to construct the connecting ring and new septum, also are produced rapidly, and there is some evidence (Crick, *et al.* 1984) that the biomineralization system is heavily stressed at this time due to the increased metabolic demands associated with these processes. It is quite plain from the position of the pillar zone in the septal neck, and from its continuity with the prismatic layer on the adapertural face of the septum (see text-fig. 2), that the pillar zone is formed during the final stages of septum formation, at about the time of body advance and metabolic stress. Thus, the widely spaced crystalline framework of the pillar zone, as well as the open, spherulitic crystal arrays of the chalky layer may represent an effort to minimize the cost of construction of these structures, or of the time necessary for their formation, by limiting the amount of carbonate in them.

We conclude by observing that maximizing attachment strength and minimizing energetic costs are not necessarily exclusive requirements. The microarchitecture of the pillar zone may serve to optimize both. It appears to us also that Kulicki and Mutvei's (1982) reconstruction of the septal cuff in *Quenstedtoceras* is consistent with the ideas set out here, and, indeed, septal neck microstructure in many fossil cephalopods may be formulated along the lines we have suggested. It is interesting to note that if our hypotheses about pillar zone function are correct, then the fluid-transporting pillar zones of endocochliates must represent a major modification of pillar zone function present in at least some ectocochliates. Determining when in cephalopod phylogeny, and by what pathways, this shift in function took place should prove to be an exciting avenue for further research.

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SEXUAL DIMORPHISM IN THE BELEMNITE *YOUNGIBELUS* FROM THE LOWER JURASSIC OF YORKSHIRE

by PETER DOYLE

ABSTRACT. Two belemnite species, *Youngibelus tubularis* (Young and Bird) and *Y. levis* (Simpson), are described from one 7·6 m bituminous shale horizon in the *falciferum* Subzone of the Yorkshire Toarcian. Ontogenetic studies show a common identity for the two species in their initial growth stages (nepionic, neanic). Divergence in morphology occurs in late growth (gerontic stage) by the development of an epirostrum in *Y. tubularis* and rostral thickening in *Y. levis*. It is concluded that *Y. tubularis* and *Y. levis* are dimorphs of a single biological species. Further, it is postulated that the epirostrum was used for counterbalancing a sexual adaptation or for courtship display purposes. Both forms are described as separate morphospecies.

DETAILED bed-by-bed collecting in the *falciferum* Subzone of the Yorkshire Toarcian has suggested a dimorphic relationship between the two belemnite species *Y. tubularis* (Young and Bird 1822) and *Y. levis* (Simpson 1855). Previously, these species have been included in different genera (e.g. Lissajous 1925; Sachs and Nalnjaeva 1975). They occur in one 7·6 m bituminous shale horizon in the mid *falciferum* Subzone. This is well exposed on the foreshore at Saltwick Bay (bed 43 of Howarth 1962). South-east of the Peak fault it is represented by the top of bed x, the Peak stones (bed xi), and the base of bed xii, which are well exposed on the foreshore between Blea Wyke Point and Peak Steel, Ravenscar.

The restriction of *Belemnites tubularis* to one horizon was recognized by most of the early workers including Simpson (1866, 1884), Phillips (1867) and Tate and Blake (1876). Notes found with the Phillips collection in the Oxford University Museum refer to a '*tubularis* bed' and the association of *Y. levis* with *Y. tubularis* was evidently known to Phillips, as specimens of *Y. levis* in the Museum are labelled: 'With *B. tubularis*, Saltwick.' Both species are usually very well preserved in this bituminous shale. It is common to find the phragmocone in place with generally the first twenty or so camerae undamaged. Pyrite commonly replaces septal walls and infills the camerae. Fine rostral detail is usually visible.

A total of eighty-three specimens of *Y. levis* and sixty-one of *Y. tubularis* have been collected by the author and Dr. P. F. Rawson, most of which are currently housed in the Department of Geology, University College London. A further forty-six specimens of *Y. levis* and thirty-five specimens of *Y. tubularis* have been examined in the collections of the British Museum (Natural History), the Oxford University Museum, and the Whitby Museum.

At present there is no comprehensive text which outlines detailed belemnite skeletal morphology. Therefore, a short glossary of the more unfamiliar terms is given below. Further details may be found in Roger (1952) and Stevens (1965).

Apical line. Axis of rostrum marked by successive positions of the apex during growth.

Compressed. Rostrum with greater dorsoventral than lateral diameter.

Conorostrid. Conical form of juvenile (nepionic) rostrum (also *Clavirostrid*, club form juvenile rostrum).

Depressed. Rostrum with greater lateral than dorsoventral diameter.

Endogastric. Ventral incurvature of the protoconch.

Epirostrum. Tube-like posterior prolongation of normal rostrum (*orthorostrum*), consisting of a central mass (*corpus pulposum*) surrounded by walls exhibiting typical belemnitid structure.

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Lateral lines. Weak linear markings on the rostral flanks possibly indicating point of fin attachment.

Ortholineate. Straight, centrally situated apical line undeflected ventrally (also *cyrtolineate*, strongly ventrally curved apical line; *goniolineate*, straight apical line close and almost parallel to venter).

Orthorostrum. True or first-formed rostrum of epirostrate belemnites, exhibiting typical concentrically layered and radially prismatic structure.

Outline. Ventral or dorsal aspect of rostrum.

Primordial rostrum. Larval (usually dish-like) rostrum attached to the distal end of protoconch.

Profile. Lateral aspect of rostrum.

The following abbreviations are used: BM, British Museum (Natural History); OUM, Oxford University Museum; WM, Whitby Museum; L, length from protoconch to apex of rostrum; D, dorsoventral diameter at the protoconch; Dl, lateral diameter at the protoconch.

SYSTEMATIC DESCRIPTIONS

Subclass COLEOIDEA Bather, 1888
Order BELEMNITIDA Zittel, 1895
Suborder BELEMNITINA Zittel, 1895
Family BELEMNITIDAE d'Orbigny, 1845

The above classification is that recognized by Jeletzky (1966) who considered the nomenclaturally invalid Polyteuthidae Stolley, 1919 to be a junior synonym of the Belemnitidae d'Orbigny. Riegraf (1980) recognized the Polyteuthidae, including within it the Belemnitidae as used by Jeletzky, plus the Cylindroteuthididae Stolley, 1919.

Subfamily MEGATEUTHINAE Sachs and Nalnjaeva, 1967
Genus YOUNGIBELUS Riegraf, 1980

Type species. B. tubularis Young and Bird, 1822.

Emended diagnosis. Very slender, moderately long to long, cylindrical to cylindriconical rostra with moderate to strong lateral compression. Transverse sections elongate subquadrate to pyriform. Apical grooves absent or residual, but apical striae commonly well developed. Epirostrum may be developed extending the total length of the rostrum to three times that of orthorostrum. Lateral lines consist of two shallow depressions separated by a weak 'weal' along the length of the orthorostrum. Apical line ortholineate, phragmocone central with slight endogastric (ventral) incurvature of the protoconch. Alveolar angle 27°.

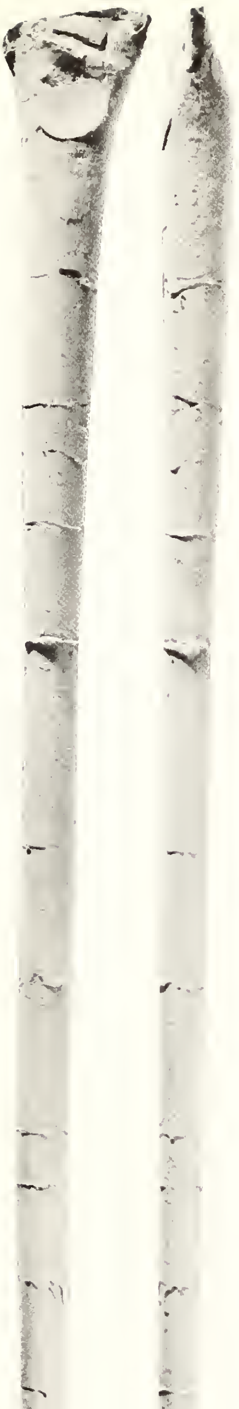
Stratigraphic range. Upper part of the lower Toarcian of Britain, Germany, France, and ?Siberia.

Discussion. Youngibelus differs from *Acrocoelites* by its lack of strong apical grooves, from *Dactyloteuthis* by its long slender cylindriconical shape and ortholineate apical line, and from *Salpingoteuthis* by its well-developed orthorostrum and lack of strong 'canals' on its flanks.

Species included are *Y. tubularis* (Young and Bird), *Y. gigas* (Quenstedt), and *Y. levis* (Simpson). *B. tripartitus gracilis* Quenstedt, assigned to *Youngibelus* by Riegraf (1980), is excluded due to its strong apical grooves. It is probably a species of *Acrocoelites.*

EXPLANATION OF PLATE 14

Figs. 1–5. *Youngibelus tubularis* (Young and Bird), ×1. 1–4, right lateral and ventral views. 1, BM C59185, neotype, epirostrum uncrushed, Saltwick. 2, BM C59186, rostrum with anterior wrinkling, epirostrum crushed, Saltwick. 3, BM C59200, rostrum with crushed epirostrum, Ravenscar. 4, BM C59199, orthorostrum with apical scar of missing epirostrum, Ravenscar. 5, BM C59192, longitudinal section (venter to right), epirostrum uncrushed, Ravenscar.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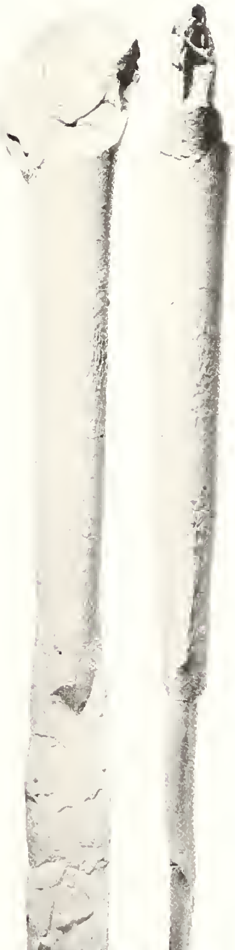
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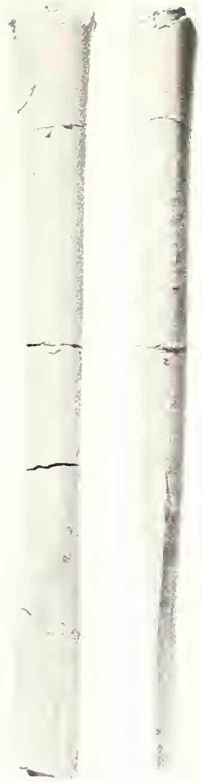
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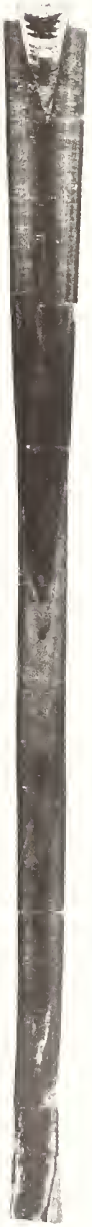
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DOYLE, *Youngibelus*

Youngibelus tubularis (Young and Bird 1822)

Plate 14, figs. 1–5

* 1822	*Belemnites tubularis* Young and Bird, p. 259, pl. xiv, fig. 6.
1829	*Belemnites tubularis* Young and Bird; Phillips, p. 163, pl. xii, fig. 20.
v1855	*Belemnites tubularis* Young and Bird; Simpson, p. 23.
v1855	*Belemnites productus* Simpson, p. 216.
vp1867	*Belemnites tubularis* Young and Bird; Phillips, p. 68, pl. xiv, fig. 36 (*non*. p″–p‴).
1920	*Cuspiteuthis tubularis* (Young and Bird); Bülow-Trummer, p. 107.
1925	*Dactyloteuthis tubularis* (Young and Bird); Lissajous, p. 148.
1969	*Belemnites tubularis* Young and Bird; Schwegler, p. 206, text-fig. 87.
1980	*Youngibelus tubularis* (Young and Bird); Riegraf, p. 149.

Diagnosis. Long *Youngibelus* with epirostrum. Outline and profile symmetrical. Transverse sections of orthorostrum pyriform to elliptical, of epirostrum almost circular. Surface of rostrum commonly wrinkled in the alveolar region.

Type specimens. Young's collection was deposited in the Whitby Museum. However, there is no evidence that any of the *B. tubularis* in the Museum were once in the possession of Young. They all bear Martin Simpson's labels and probably were collected by him. One specimen, No. 678, is similar in some respects to Young and Bird's pl. xiv, fig. 6, but it has been remounted on a block of shale with large numbers of crushed Dactylioceratids. This also was apparently collected from High Whitby and not Saltwick. With no proven syntypes remaining from which to select a lectotype, a neotype is here designated.

Young and Bird's *stratum typicum* is the 'Alum Shale' of Saltwick: 'Alum Shale' embraced the whole of the Upper Lias. The beds exposed in Saltwick Bay are of *falciferum* Subzone, with bed 43 (Howarth 1962) exposed on a large proportion of the shore. As *B. tubularis* is common within this horizon it can be assumed that Young obtained his syntypes here. Hence specimen BM C59185 (Doyle Collection) (Pl. 14, figs. 1, 2) from bed 43 of Saltwick is designated neotype.

Locality and material. Saltwick Bay and Ravenscar, *falciferum* Subzone (bed 43 and its equivalents of Howarth 1962). BM thirty-four specimens: Blake Collection (C11985–11987), Wright Collection (C42212–42215), and C9681–9685, C2288 (ten specimens), C3655, 15996, 15997, 37596, C57355, C405 (two specimens), 83687, 88949. OUM, seven specimens: Phillips Collection (J38036, J38037, J15101, J15108, J15109) and J38274, J37676. WM, six specimens: old no. 59, no. 678, and four unregistered.

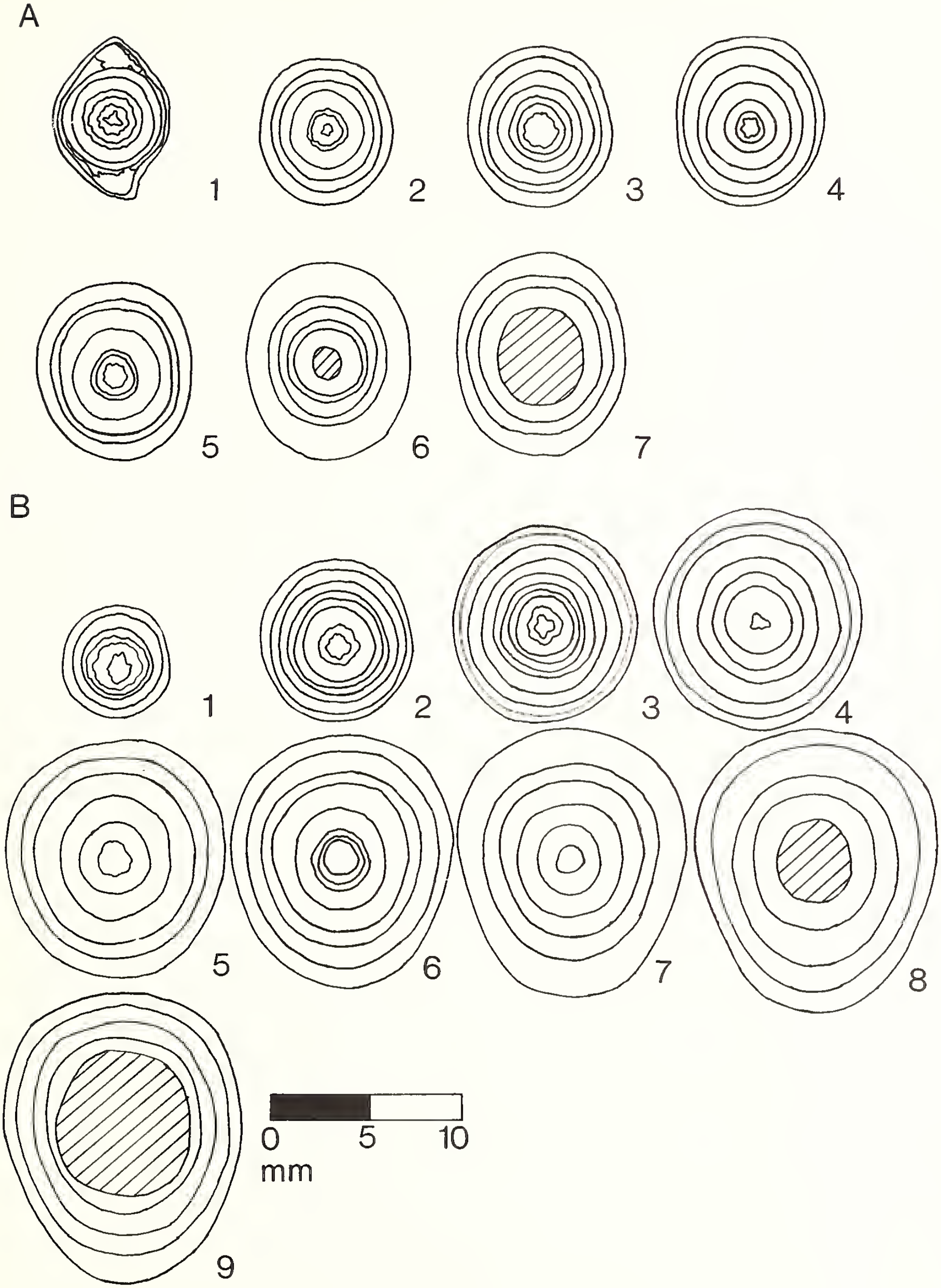
Description. Rostrum very elongate and slender, length of the orthorostrum about six times that of the transverse diameter at the protoconch. Dimensions of figured section: L, 61·5 mm; D, 9·6 mm; Dl, 7·5 mm. The outline is symmetrical and subcylindrical, with a slight adoral flaring. The apex of the orthorostrum is mucronate and slightly attenuate protruding into the epirostral fabric. The apex of the epirostrum is generally compressed, but where it is preserved it is acute, with very gentle divergence. The profile is less symmetrical than the outline, with a slightly more inflated venter. A constriction tends to develop where the epirostral wall meets the orthorostrum. This gives the impression of flaring from the almost cylindrical epirostrum.

Transverse sections reveal that the orthorostrum is generally compressed for most of its length, the epirostrum less so. There is no marked depression of the rostrum. The sections of the orthorostrum are pyriform in shape. No apical grooves are present, but apical striae are commonly well developed. Those on the apex of the orthorostrum may be more incised than those on the apex of the epirostrum.

Wrinkles of the surface of the rostrum at the alveolar end are a common trait of this species; more extreme examples were separated by Simpson (1866) as *B. productus*. Lateral lines take the form of long shallow areas in a ventrolateral position. These are separated by a 'weal', common to most members of the Megateuthinae.

The phragmocone occupies a central position with the protoconch slightly incurved ventrally. The phragmocone penetrates approximately one-third of the orthorostrum. The apical line is ortholineate, the alveolar angle 27°.

Structure of the ortho- and epirostrum. The orthorostrum consists of concentric growth layers of laminae pellucidae (light unobscured calcite). The walls of the epirostrum consist of the same material. These thin (0.5 mm) epirostral walls form a tube which is filled with an apparently structureless porous mass (*corpus pulposum* of Muller-Stoll 1936). Where they join the orthorostrum, the epirostral walls become its last concentric growth lamellae. The apical third of the orthorostrum protrudes into the epirostral 'cavity'. This 'cavity' is



TEXT-FIG. 1. Transverse sections of *Youngibelus tubularis* and *Y. levis* from Saltwick Bay. Sections at 5 mm intervals (section numbers indicating approximate length). Alveolus hatched. Venter lowermost. A, *Y. tubularis*, BM C59190, sections 1–8 of orthorostrum. The epirostrum is crushed in the lateral plane (section 1). B, *Y. levis*, BM C59198, sections 1–11 of rostrum.

infilled with a highly porous and granulose mass, which seems to have crude growth lines mimicking the apex of the orthorostrum. No trace of the radiating, recrystallized prisms of the orthorostrum are seen here, although holes in the epirostral mass indicate diagenetic alteration (Spaeth, Hoefs and Vetter 1971).

Ontogeny

Transverse sections. The terms nepionic, neanic, and ephebic–gerontic introduced by Fischer (1947) and discussed by Pugaczewska (1961) are used to describe the ontogeny. The section of the nepionic stage is pyriform with the venter broadest. This stage, like all subsequent stages, has strong striae at its apex, giving a corrugated aspect to the growth lines (text-figs. 1A, 2A). The neanic growth stage marks a departure from a pyriform to a more elliptical section. In the alveolar region the section is characterized by a more quadrate shape, changing to an elongate ellipse in the stem region. The change from the nepionic pyriform to neanic elliptical section is gradual. The apex is striated (text-fig. 1A, 2A). The ephebic–gerontic stage shows a reversion to a pyriform section, although less pronounced than in the nepionic stage. However, in this stage the dorsum is broadest, a complete reversion from the nepionic stage (text-figs. 1A, 2A). The gerontic stage includes the development of the epirostrum, epirostral walls becoming the final growth layers. Sections of the epirostrum have an almost circular shape.

Longitudinal sections. The nepionic growth stage of *Y. tubularis* has a conorostrid (conical) form. The neanic stage is represented by a more elongate form of the nepionic rostrum. The ephebic–gerontic growth stage is characterized by a rapid elongation of the rostrum, culminating in the development of an epirostrum. The last growth layers of the orthorostrum display this elongation with respect to the width. Development of the epirostrum was obviously a late-stage feature (see also Krimholz 1958), the epirostral walls growing out from the orthorostrum, followed by the infilling of the epirostral cavity. Text-fig. 3 shows the dramatic change from allometric to very strongly allometric growth in the ephebic–gerontic stage.

Discussion. Zieten's (1831) *B. longissimus* Miller closely resembles uncrushed specimens of *Y. tubularis*. Quenstedt's (1848) *B. acuarius tubularis* also appears to belong to *Y. tubularis*; the long ventral groove evident in the figure may well be pathological. The specimen figured by Phillips (1867, pl. xiv, fig. 36 p″–p‴) is probably *Y. gigas* (Quenstedt). Werner's (1912) synonymy of *B. tubularis* included forms with pronounced apical grooves such as *B. tripartitus gracilis* Quenstedt and therefore his definition of the species only partly applies to the present one.

Youngibelus levis (Simpson, 1855)

Plate 15, figs. 1–6

non 1836 *Belemnites laevis* Roemer, p. 165.
v *1855 *Belemnites levis* Simpson, p. 25.
v 1867 *Belemnites laevis* Simpson; Phillips, p. 57, pl. x, figs. 21, 25.
v 1883 *Belemnites simpsoni* Mayer-Eymar, p. 641.
1920 *Cuspiteuthis laevis* (Simpson); Bülow-Trummer, p. 103.
1925 *Acrocoelites laevis* (Simpson); Lissajous, p. 103.

Diagnosis. Medium-sized *Youngibelus* without epirostrum. Outline symmetrical, profile nearly symmetrical, venter slightly inflated. Transverse sections pyriform.

Type specimens. Three syntypes are in the Whitby Museum (453a, b, c). All three display crushed apices. Syntype 453c is poorly preserved with greater than average compression; 453b has abnormally enlarged apical depressions; 453a is reasonably well preserved and displays all the common features associated with this species—it is here designated lectotype. This is probably the specimen figured by Phillips (1867, pl. x, fig. 23 l″).

EXPLANATION OF PLATE 15

Figs. 1–6. *Youngibelus levis* (Simpson), × 1. 1, 2, 4, 5, right lateral and ventral views. 1, 2, BM C59198, 59196, rostra from Ravenscar. 3, BM C59195, longitudinal section (venter to left), apex uncrushed, Saltwick. 4, 5, BM C59197, 59188, rostra from Saltwick. 6, BM C59191, longitudinal section (venter to left), apex crushed, Ravenscar.

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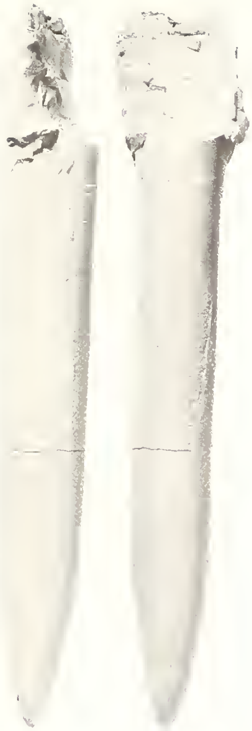

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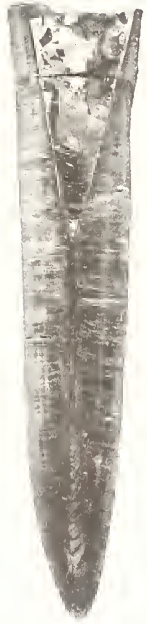

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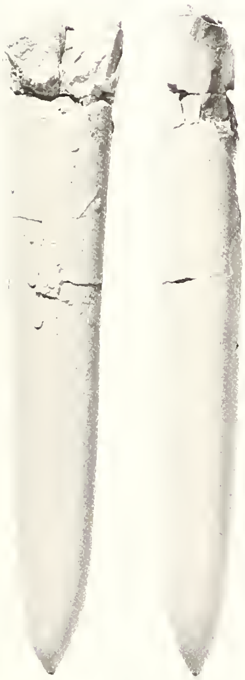

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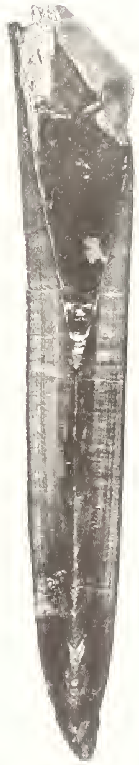

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DOYLE, *Youngibelus*

The syntypes were all collected from the 'Jet Rock, Upper Lias, near Whitby' (Simpson 1855, p. 25). This was later refined by Simpson (1884) to 'Division 5b, Upper Lias' (equivalent to bed 43 of Howarth 1962) from Saltwick. These specimens were later incorrectly labelled as coming from the '*communis*' Zone, Saltwick; beds exposed at Saltwick are of the *falciferum* Zone and Subzone.

Locality and material. Saltwick Bay and Ravenscar, *falciferum* Subzone (bed 43 and its equivalents of Howarth 1962). BM, seventeen specimens: Bean Collection (one, unregistered), Blake Collection (C11940-11942, C11944-11946), Wright Collection (C42218-42222, C42238, C42241) and C57090-57092. OUM, twelve specimens: Phillips Collection (J15258, J15260-15264, J15275, J15287-15289). WM, seventeen specimens: Simpson Collection (old nos. 453a, b, c; new nos. 332, 334, 335, 336, 337, 345-350, 358a, b, c).

Description. Rostrum of moderate size and generally slender, length about four times that of the transverse diameter at the protoconch. Dimensions of figured section: L, 47 mm; D, 13.5 mm; Dl, 11 mm. The outline is symmetrical and subcylindrical. The apex terminates rapidly (0.2 of total length), leaving the rest of the outline cylindrical. The profile is slightly less symmetrical than the outline, the venter generally more inflated than the dorsum. The profile is cylindriconical but with a general resemblance to the outline.

The transverse sections are compressed throughout the length of the guard, the emphasis shifting from dorsolateral to ventrolateral compression adorally. The sections are pyriform, with a broad venter. Depression is not marked in this species but may be developed in some individuals to a small degree. No definite apical grooves are present but the presence of slight depressions gives the impression of dorsolateral grooves. The apex is usually characterized by fine striations surrounding it. Lateral lines take the form of long flat areas subdivided into two subdepressions separated by a 'weal'.

The phragmocone is central, with the protoconch slightly endogastrically incurved. The phragmocone pentrates a third of the way into the rostrum. The apical line is ortholineate and the apical angle 27°.

Ontogeny

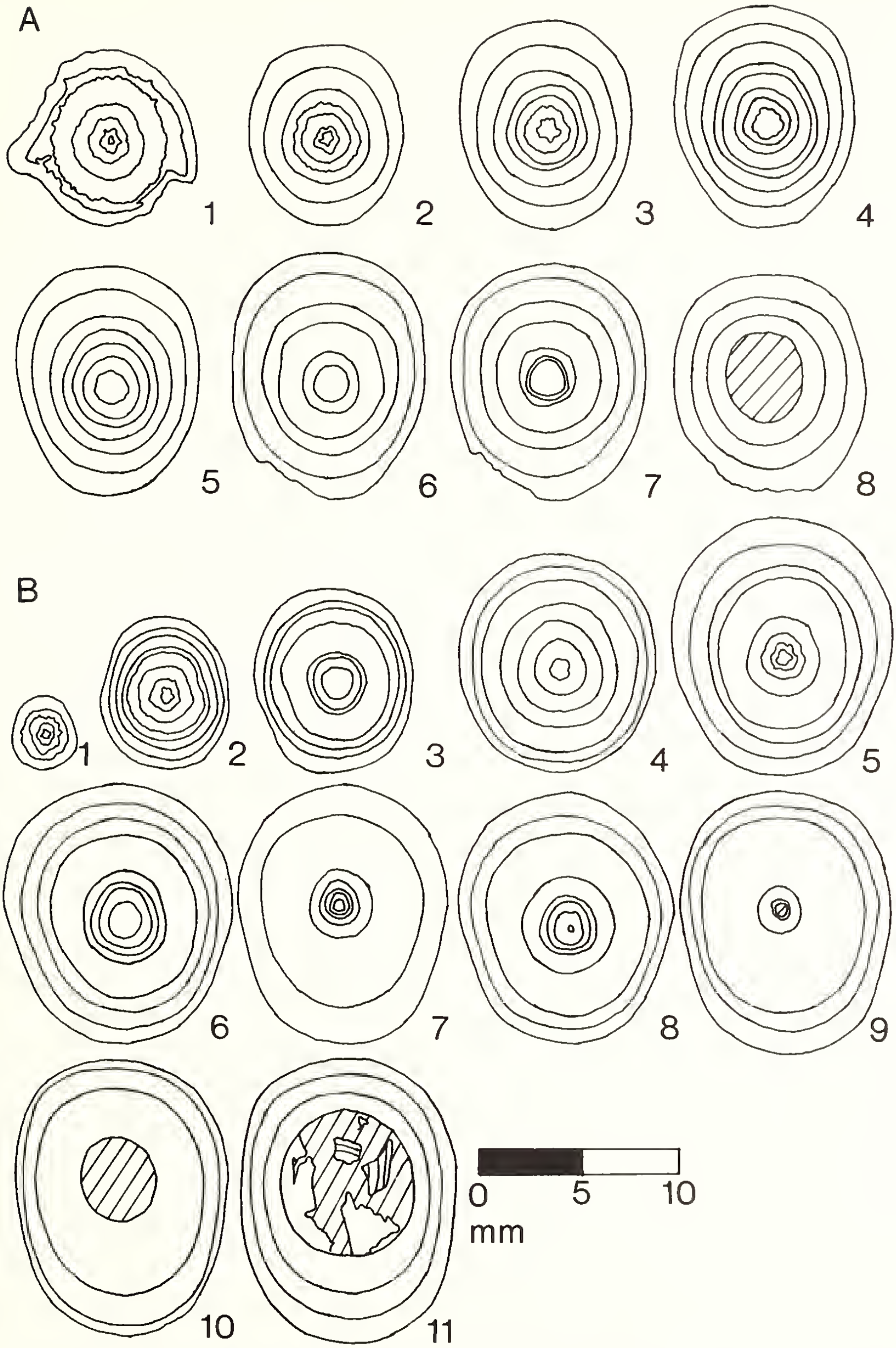
Transverse sections Three stages are recognized. The nepionic stage is characterised by a pyriform section with its maximum breadth at the venter. The apex is striated as in all subsequent stages (text-figs. 1B, 2B). The neanic stage shows a progression away from the pyriform section of the nepionic stage towards a more elliptical to subquadrate section (text-figs. 1B, 2B). This stage is also striated at the apex. In the ephebic-gerontic stage the surface morphology of the adult rostrum displays a section varying with its position relative to the rostrum. The apical region reveals a section which is pyriform resembling that of the nepionic stage. This is due to dorsolateral apical depressions. The stem region has a pyriform section with the dorsum broadest, a reversal from the neanic stage. This corresponds to an increasing ventrolateral compression adorally (text-figs. 1B, 2B.).

Longitudinal sections. The nepionic rostrum has a generally short conorostrid form. Growth proceeds in the neanic stage allometrically, but with relative increases of width to length. Gerontic growth is strongly allometric (text-fig. 3) with width increasing at a much greater rate than length. This results in a much stouter rostrum in the gerontic stage.

Discussion. This species closely resembles two described by Simpson (1855, 1884): *B. aptus* and *B. trivialis*. *B. aptus* may be an aberrant *Y. levis* with quite prominent apical grooves. *B. trivialis* has a similar shape and form, with apical striae and may be a juvenile *Y. levis* (as suggested by Phillips 1867 and Blake *in* Tate and Blake 1876).

B. levis Simpson was formerly considered to be a primary homonym of *B. laevis* Roemer. However, Simpson's original spelling omitted the 'a' attributed to this species by other authors. This one letter difference validates *B. levis* Simpson according to the International Code of Zoological Nomenclature. *B. simpsoni* Mayer-Eymar, erected to replace the homonym, therefore becomes a junior objective synonym of *B. levis* Simpson. *B. levis* was formerly placed in the genus *Acrocoelites* presumably due to its stratigraphical association with species of this genus and its differences from other Liassic genera. Lateral lines seen on *B. levis* are common in most members of the Megateuthinae. Sachs and Nalnjaeva (1975) transferred it to *Mesoteuthis*, presumably due to a lack of apical grooves. Bülow-Trummer (1920) came closest to identifying its true affinities when he placed the species in *Cuspiteuthis*.

B. levis is herein attributed to the genus *Youngibelus* for the following reasons: the species lacks apical grooves but has well-developed apical striae; it has a slender cylindrical shape with lateral compression and an ortholineate apical line; the central phragmocone is characteristic of the genus.

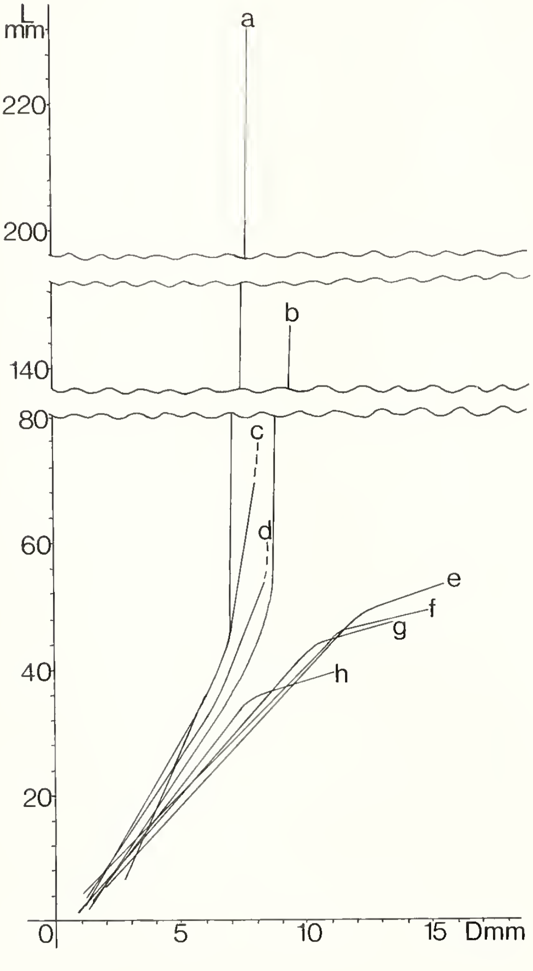


TEXT-FIG. 2. Transverse sections of *Youngibelus tubularis* and *Y. levis* from Ravenscar. Sections at 5 mm intervals (section numbers indicating approximate length). Alveolus hatched. Venter lowermost. A, *Y. tubularis*, BM C59194, sections 1–7 of orthorostrum. The epirostrum is crushed in the dorsoventral plane (section 1). B, *Y. levis*, BM C59193, sections 1–9 of rostrum.

THE ONTOGENY OF *Y. LEVIS* AND *Y. TUBULARIS*

The protoconch and primordial rostra take the same form in both species (text-fig. 3). The protoconch is nearly spherical, being slightly endogastrically incurved with respect to the rest of the phragmocone. The primordial rostrum is in the form of a dish attached to the distal end of the protoconch. This type of primordial rostrum is commonly seen in members of the Belemnitina (Jeletzky 1966, p. 130).

The nepionic rostra of *Y. levis* and *Y. tubularis* are conorostrid, developing a more elongate version of this in the neanic stage which is also identical in both species. Postneanic development signals the change in form of both *Y. levis* and *Y. tubularis*. In the gerontic stage of *Y. tubularis* there is a relatively rapid increase in the length of the orthorostrum, with little change in the maximum diameter. The epirostrum is then developed, rapidly increasing the length of the whole rostrum by a factor of three. The epirostrum is an outgrowth of the final layers of the orthorostrum, the epirostral walls also covering the orthorostrum. This outgrowth was followed by the infilling of the epirostral cavity by the *corpus pulposum*. The gerontic stage of *Y. levis* is characterized, on the other hand, by the formation of a much stouter rostrum, the length increasing only slightly. This contrast between the two styles of gerontic development is well illustrated by the growth curves in text-fig. 3. Here



TEXT-FIG. 3. Growth curves of *Youngibelus tubularis* and *Y. levis*. *Y. tubularis*: *a*, BM C59214, *b*, BM C59192, *d*, BM C59217 (Ravenscar); *c*, BM C59218 (Saltwick). Specimens *c* and *d* have crushed epirostra, most of which are lost. *Y. levis*: *f*, BM C59195 (Ravenscar); *e*, BM C59191, *g*, BM C59216, *h*, BM C59215 (Saltwick).

the curves point to a practically identical early development with differentiation in the final growth stages. Differences between the early growth curves are due to specific variation, the variance within the *Y. tubularis* group being as great or greater than the differences between both species.

In transverse section the nepionic rostra of both species are pyriform with their maximum width at the venter. The neanic stage shows a more neutral elliptical section in both *Y. tubularis* and *Y. levis*. From here *Y. tubularis* develops a pyriform section with the dorsum widest. The increase in diameter of the rostrum is relatively small considering the great length attained in the gerontic stage. *Y. levis* has a similar pyriform section, but the increase in diameter is greater than that in *Y. tubularis*, corresponding to a relatively small increase in length.

It would seem, therefore, that before the gerontic stage the juveniles of both *Y. levis* and *Y. tubularis* are exactly alike in all aspects. After the neanic stage (the onset of sexual maturity) the two forms become separate. Throughout ontogeny the apical line remains central and the alveolar angle differs little between the two species.

SEXUAL DIMORPHISM

d'Orbigny (1842) was the first author to point to the possibility of differences between the sexes in belemnites. Subsequently the hypothesis has been touched upon by Phillips (1867), Lissajous (1925), Roger (1952), Waterston (1952), Delattre (1956), Stevens (1965), and Pinckney (1975). It is accepted that modern cephalopods show dimorphic characters to a greater or lesser degree (Westermann 1969) and the hypothesis of dimorphism in ammonites is also widely accepted (e.g. Makowski 1963; Callomon 1963; Palframan 1966). It therefore seems reasonable to expect dimorphism in belemnites.

Dimorphism in modern cephalopods takes the form of differences in size and this is also a common feature in ammonites. In belemnites, the function of the rostrum is seen primarily as a counterbalance for the main mass of the body tissue, head, and arms. If one sex were larger than the other, an increase in size of the rostrum to counterbalance the increased bulk of the body would be expected. The rostrum would be directly affected by sexual dimorphism manifested as a difference in size. d'Orbigny (1842), Waterston (1952), and Delattre (1956) claim to have recognized large and small forms of similar belemnites which they claim are dimorphic.

However, some workers (Stevens 1965; Pinckney 1975) believe that dimorphic characters would be more likely to occur beneath the pro-ostracum, where it is presumed the gonads were housed. They suggest that differences in length and form of belemnite rostra are more likely to be due to intraspecific variation. Riegraf (1981, p. 125) believed that it is difficult to recognize adult micro- and macrorostra. He cited as an example *Y. tubularis*, for which no microrostrum could be found.

Makowski (1963) outlined four conditions which he considered prerequisites for the acceptance of dimorphism in ammonites:

1. Identical initial stages of ontogeny in both, with the identity of their phylogeny.
2. Lack of intermediate forms in the adult stages.
3. Presence of both forms in the same strata.
4. Numerical ratio of the two supposed sexes (sex ratio) comparable to that observed in living forms.

These criteria are also applicable to belemnites. As shown above, the ontogeny of *Y. tubularis* and *Y. levis* is identical in nepionic and neanic stages, differences only becoming apparent in the gerontic stage. Phylogenetically, both species have apparent parallel development, arising from the acrocoelitid root stock (see Schwegler 1962). There are no intermediates between the adult growth stages of *Y. tubularis* and *Y. levis*. The presence of crushed apices in some examples of *Y. levis* cannot be accepted as true epirostral development; it may be due to the resorption of growth layers as described by Muller-Stoll (1936) and Pugaczewska (1961). The stout *Y. levis* with slightly crushed apex cannot be described as intermediate between *Y. levis* with normal apex and the much more elongate and slender *Y. tubularis*.

Neither species has been found above or below bed 43 (*falciferum* Subzone) of Saltwick or its equivalents at Ravenscar. Both forms have been reported together from similar horizons in West Germany (Riegraf, pers. comm.). The sex ratios for the two associations at Ravenscar and Saltwick are 1·0 : 1·1 and 1·0 : 1·2 respectively. This is within acceptable limits for similar modern coleoid associations (Mangold-Wirz 1963).

FUNCTION OF THE EPIROSTRUM

The precise function of the epirostrum has remained a mystery for many years. Some authors (Muller-Stoll 1936; Roger 1952) suggested that it represents the last in a series of growth stadia occurring in all belemnites. Krimholz (1958) believed that its formation was almost accidental, due to a sudden elongation of the mantle, and that it cannot be tied down to any particular function. Recent authors (Jeletzky 1966; Seilacher and Wiesenauer 1978) believe that the epirostrum functions as a balancing aid, developed only in certain lineages where extra balance is required.

d'Orbigny (1842) suggested that the development of epirostra in *Dactyloteuthis acuarius* (Schlotheim) was due to sexual dimorphism, the microrostrum being *D. irregularis* (Schlotheim). It is probable that this is the case (other examples include *Pleurobelus*; *P. lagenaeformis* (macrorostrum), *P. compressus* (microrostrum), and *Youngibelus*). The epirostrum may fulfil a need to balance some specialized sexual adaptation in the male or female. The male may have had a rather elongate or bulky hectocotylized arm, or the female a brood pouch or similar structure. In either case the centre of gravity would have been affected. It could be that the increased size of one of the sexes may be for visual display used in courtship, as in some modern cephalopods. The relatively light construction and rapid growth of the epirostrum would be suitable for these purposes.

The lack of epirostra in other belemnite groups may point to different levels of specialization. d'Orbigny (1842) described two types of dimorphism; simple and complex (without and with epirostra respectively). The simple type includes dimorphs with relatively small differences in size, and examples have been described by d'Orbigny (1842), Waterston (1952), and Delattre (1956). It may reflect less need for counterbalancing than 'complex' dimorphism. The adult size relationship of the sexes is extremely variable down to the genus level in modern cephalopods (Westermann 1969, p. 19), and this 'simple' and 'complex' dimorphism may represent a similar relationship.

TAXONOMIC IMPLICATIONS

Most ammonite workers (e.g. Makowski 1963; Palframan 1966) consider that dimorphic pairs should be included in one single biological species. However, in the present study the dimorphs are considered separately under two specific names, here included in the same genus (see Callomon 1963).

The startlingly different surface morphologies of the two forms in some way justifies this rather artificial method. As suggested, dimorphism in belemnites may well be on differing levels of complexity and it is probable that most examples are less easy to recognize than the one studied. Therefore, until more dimorphic pairs are recognized it is considered more worth while to retain the separate names, relating to morphospecies, rather than confuse this more practical method by inclusion into one closely defined biological species.

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THE EARLIEST KNOWN FENESTRATE BRYOZOAN, WITH A SHORT REVIEW OF LOWER ORDOVICIAN BRYOZOA

by PAUL D. TAYLOR *and* GORDON B. CURRY

ABSTRACT. Silicified residues from the late Arenig Tourmakeady Limestone of County Mayo, Ireland, contain a new bryozoan, *Alwynopora orodamnus* gen. et sp. nov. Colonies have erect branches bearing two rows of alternating zooecial apertures on their frontal surface and barren of apertures on their reverse surface. Branches bifurcate irregularly, successive bifurcations tending to be approximately in the same plane. There is a strong gradient of branch thickening towards the colony base. *Alwynopora* is the earliest known bryozoan of the Order Fenestrata. The occurrence of bryozoans in the lower Ordovician is briefly reviewed; the thirty-eight taxa described have an extensive taxonomic distribution, are morphologically diverse, and geographically widespread.

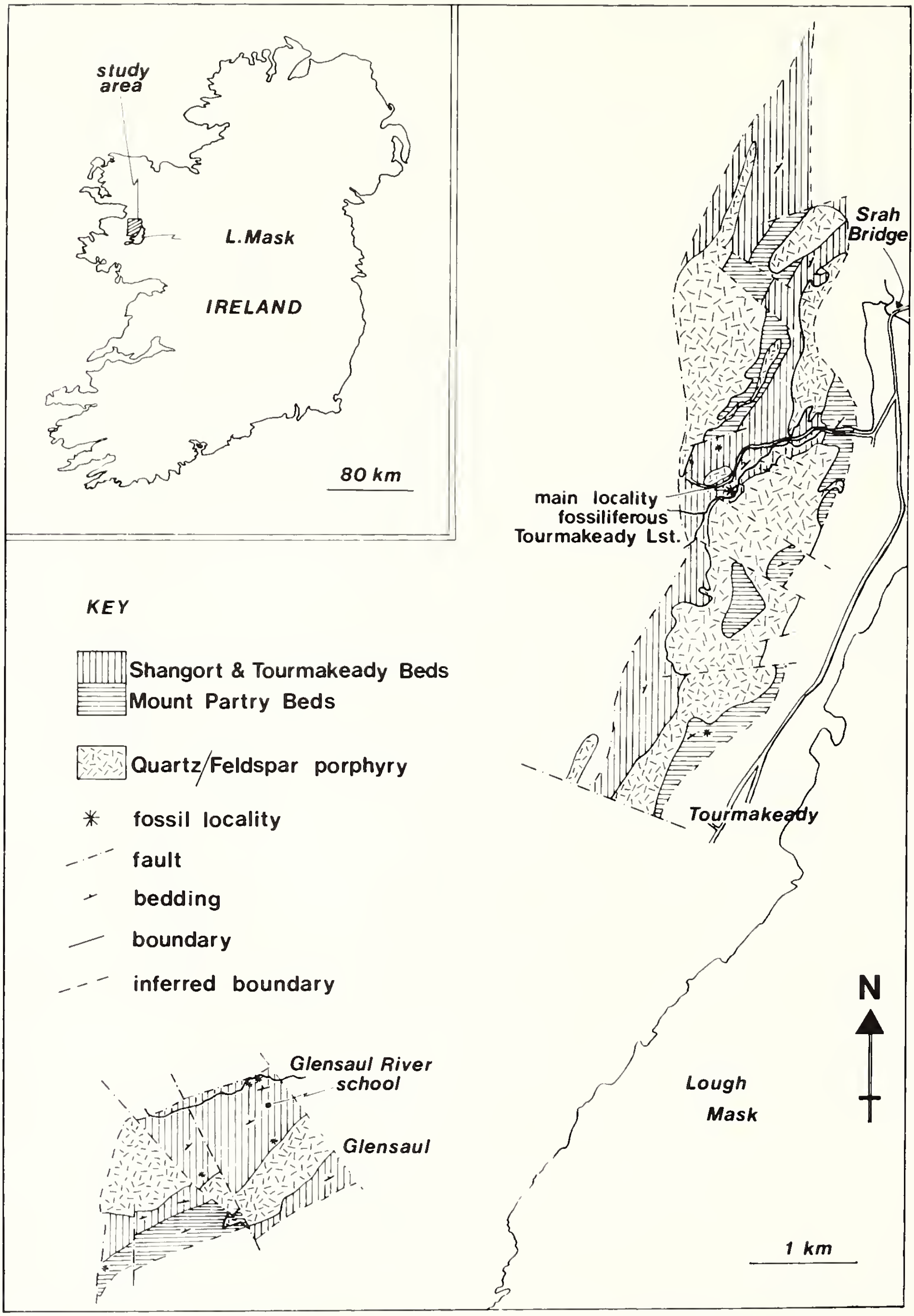
THE Fenestrata are regarded as a distinct order of stenolaemate bryozoans in the revised *Treatise on invertebrate paleontology* (Boardman *et al.* 1983), although some bryozoologists argue for their retention as a suborder of the Cryptostomata (Blake *in* Boardman *et al.* 1983). Most fenestrates are readily recognizable by their reticulate or pinnate colonies with zooecial apertures opening on one side of the branches only. Fenestrate bryozoans peaked in diversity during the late Palaeozoic when members of the families Fenestellidae and Acanthocladiidae dominated the majority of bryozoan faunas. However, the origins of the order may be traced back to the Ordovician. Hitherto the earliest described fenestrate bryozoan dates from the middle Ordovician. The purpose of this paper is to describe the first lower Ordovician fenestrate bryozoan, *A. orodamnus* gen. et sp. nov., from the Tourmakeady Limestone of western Ireland. In the absence of unequivocal Cambrian bryozoans, the earliest bryozoans are a modest number of taxa described from the lower Ordovician. The discovery of this new fenestrate bryozoan adds to the taxonomic distribution, morphological diversity, and geographical range of lower Ordovician bryozoans which are briefly reviewed.

All described material bears British Museum (Natural History) (abbreviated BM (NH)) registration numbers.

GEOLOGICAL SETTING

The lower Ordovician Tourmakeady Limestone (Glensaul Group) of Co. Mayo, Ireland, is of considerable interest not only because of the abundance and diversity of the fossils it contains, but also because this fauna provides a link between contemporaneous American province faunas in Scotland, North America, and Spitsbergen. The stratigraphic setting of the Tourmakeady Limestone within the lower Ordovician inliers north of Lough Mask (text-fig. 1) was first described by Gardiner and Reynolds (1910), although at that time the abundance of the indigenous shelly fossils was not appreciated, and the rich assemblages were not subjected to full taxonomic investigation. Gardiner and Reynolds did, however, recognize the stratigraphic importance of the inliers, and their age determinations were based on lists of graptolitic and shelly faunas collected from various exposures within the Tourmakeady and Glensaul successions. The graptolite faunas have been reinvestigated (Dewey *et al.* 1970) following the discovery of some new localities. In addition, the rich brachiopod faunas have now been studied (Williams and Curry 1984), and descriptions of the associated trilobites are in preparation.

[Palaeontology, Vol. 28, Part 1, 1985, pp. 147–158.]


study area
L. Mask
IRELAND
80 km
KEY
Shangort & Tourmakeady Beds
Mount Partry Beds
Quartz/Feldspar porphyry
fossil locality
fault
bedding
boundary
inferred boundary
Glensaul River
school
Glensaul
Srah Bridge
main locality fossiliferous Tourmakeady Lst.
Tourmakeady
Lough Mask
N
1 km

TEXT-FIG. 1. Geological map of the Glensaul Group (Arenig) in Co. Mayo, Eire, showing the Tourmakeady Limestone locality.

The great diversity and abundance of the Tourmakeady Limestone fauna was not fully appreciated until it was discovered that the indigenous fossils have been silicified. As a result, intensive collecting by Sir Alwyn Williams yielded over 2 tons of silicified limestone, which was subsequently etched to give over 10,000 silicified or chitino-phosphatic brachiopods and smaller numbers of silicified trilobites, gastropods, bryozoans, and crinoids. The Tourmakeady Limestone occurs as isolated blocks within well-bedded calcareous tuffs and grits, which together constitute the Shangort and Tourmakeady Beds of Gardiner and Reynolds (see text-fig. 1). Non-silicified fossils, in particular brachiopods and trilobites, are also found at several localities within the tuff and grit succession, and are conspecific and almost certainly contemporaneous with the silicified fossils in the limestone. However, the non-silicified fossils are generally in a poorer state of preservation, and indeed no well-preserved bryozoans have been recovered from the clastic sediments. The available material, therefore, consists entirely of silicified specimens recovered from etched residues.

Stratigraphically the Tourmakeady Limestone and surrounding sediments occur above an uppermost lower Arenig graptolite assemblage ascribed to the *Isograptus gibberulus* Zone, and are overlain by an upper Arenig assemblage of the *Didymograptus hirundo* Zone (Gardiner and Reynolds 1909, 1910; Dewey *et al.* 1970). This is consistent with age determinations based on the shelly fossils from the Tourmakeady Limestone, which also indicate an upper Arenig age, equivalent to zone K of the North American biostratigraphic succession (see table in Curry *et al.* 1982).

The Tourmakeady Limestone is thought to represent the disrupted remnants of an offshore carbonate buildup, perhaps deposited peripheral to submarine volcanic accumulations (Williams and Curry 1984). The indigenous fauna shows no signs of significant post-mortem transportation, and hence the majority of the benthic animals are assumed to have colonized a fine-grained calcareous mud substrate, subjected to gentle water currents and low to moderate sediment accumulation rates. In keeping with this interpretation, many brachiopods show morphological adaptations for a freelying mode of life (Williams and Curry 1984), while other pedunculate forms can realistically be assumed to have developed modifications of pedicle form to achieve anchorage in fine-grained substrates (as happens in Recent forms, e.g. Curry 1981, 1983).

SYSTEMATIC PALAEONTOLOGY

Indeterminate ?bryozoan

Text-fig. 2A

Material. BM(NH) PD6230.

Description. A poorly preserved fragmentary fossil bearing contiguous, oval-shaped apertures about 0·40 × 0·25 mm in diameter.

Remarks. This may be a fragment of a bryozoan colony, probably either a cystoporate or a trepostome.

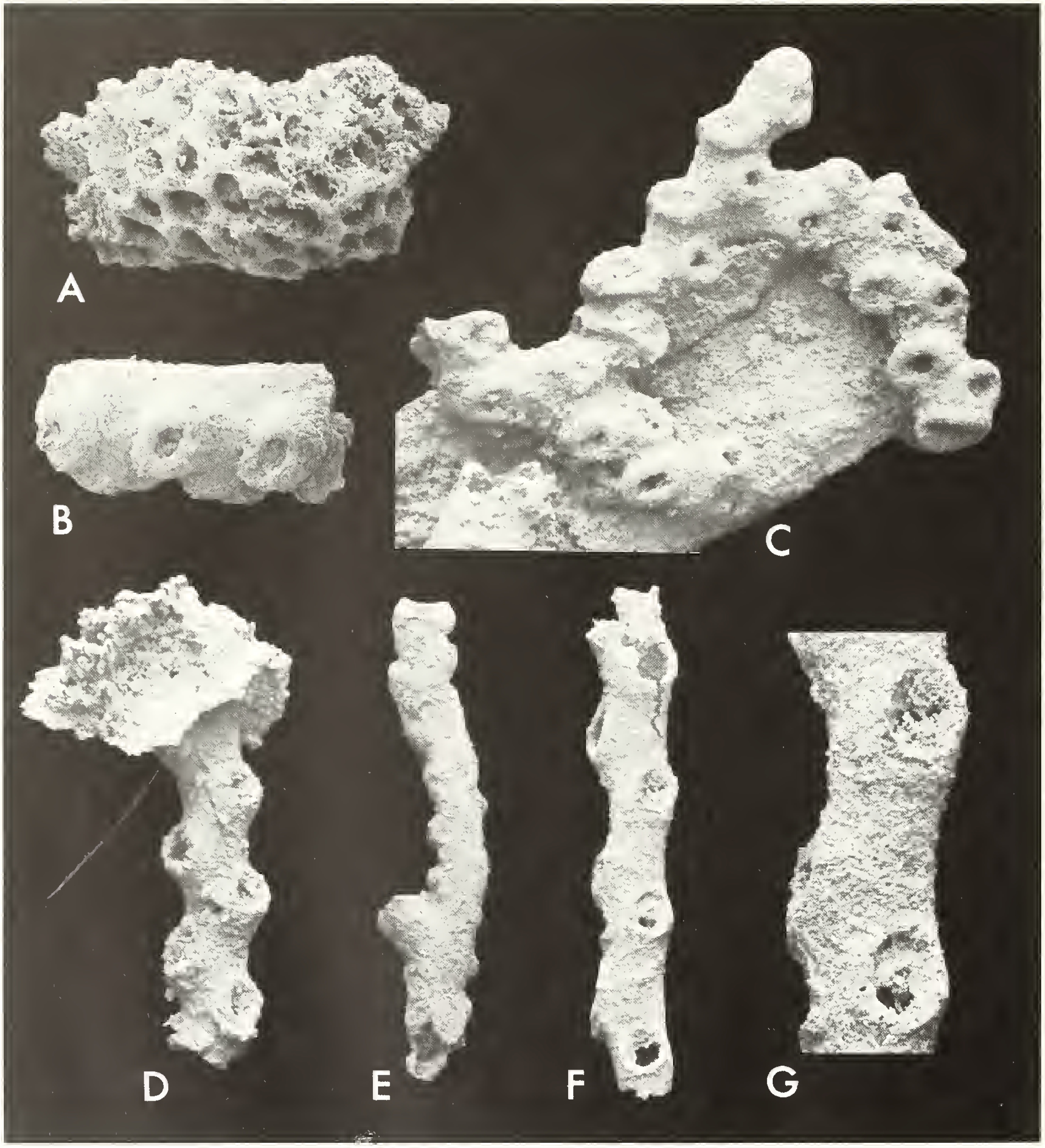
Distribution. Tourmakeady Limestone (upper Arenig), Tourmakeady, Co. Mayo, Eire.

Order FENESTRATA Elias and Condra, 1957
?Family ENALLOPORIDAE Miller, 1889
Genus ALWYNOPORA gen. nov.

Type species. A. orodamnus sp. nov.

Derivation of name. After Sir Alwyn Williams who collected the silicified limestone containing this new bryozoan.

Diagnosis. Fenestrata with branches bifurcating irregularly, usually in one plane, anastomosing occasionally, and becoming considerably thickened towards the colony base; two longitudinal rows of alternating zooecial apertures are borne on the frontal surface of each branch.



TEXT-FIG. 2. Bryozoans from the Tourmakeady Limestone. A, indeterminate ?bryozoan, BM(NH) PD6230, × 17. B–G, *Alwynopora orodamnus* sp. nov. B, lateral view of compressed branch with frontal surface lowermost, BM(NH) PD6235, × 23; C, bifurcating fragment, BM(NH) PD6241, × 20; D, holotype with encrustation at distal end, BM(NH) PD6231, × 27; E, reverse surface of branch lacking apertures, BM(NH) PD6265, × 10; F, G, frontal surface of narrow, slightly compressed branch, BM(NH) PD6259, F, × 25, G, × 56. (Scanning electron micrographs: A, B, gold-coated specimens using secondary electrons; C–G, uncoated specimens using back-scattered electrons.)

Alwynopora orodamnus sp. nov.

Text-figs. 2B–G, 3, 4

Holotype. BM(NH) PD6231.

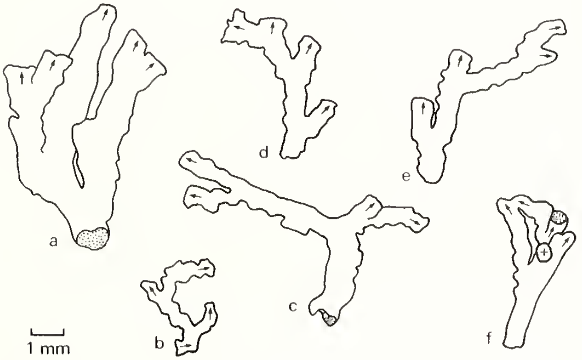
Paratypes. BM(NH) PD6232–6272.

Occurrence. Tourmakeady Limestone (upper Arenig), Tourmakeady, Co. Mayo, Eire.

Derivation of name. Orodamnus, Greek meaning bough or branch.

Diagnosis. As for genus.

Description. Colonies have been recovered only as branch fragments which bifurcate unequally or, more rarely, dichotomously. Both bifurcation angle (mean = 50°, range = 30–135° from twenty-one determinations) and interval between bifurcations (mean = 1·73 mm, SD = 0·890 mm, range = 0·40–4·05 mm from nineteen determinations) are very variable. Although anastomoses between branches may be observed, they are neither abundant nor regular. Branches are subcircular to ovoid in transverse section. Two rows of non-contiguous zooecial apertures open on one surface of the branch. Apertures on either side of this frontal surface alternate. Interapertural spacing measured along the branch averages 0·54 mm (SD = 0·088 mm, range = 0·45–0·75 mm from twenty-five colonies). Branch width and depth are highly variable with the thickest branches over three times wider than the thinnest (mean width = 0·62 mm, SD = 0·210 mm, range = 0·32–1·08 mm from twenty-five colonies). Some fragments show a proximal to distal gradient of decreasing branch width. Branch margins are gently sinuous in narrow branches, sinuosities corresponding to the positions of protruberant zooecial apertures, but straight-sided in thick branches. Striae or other branch ornamentation have not been observed. Possible colony bases are slight, flat-bottomed expansions.

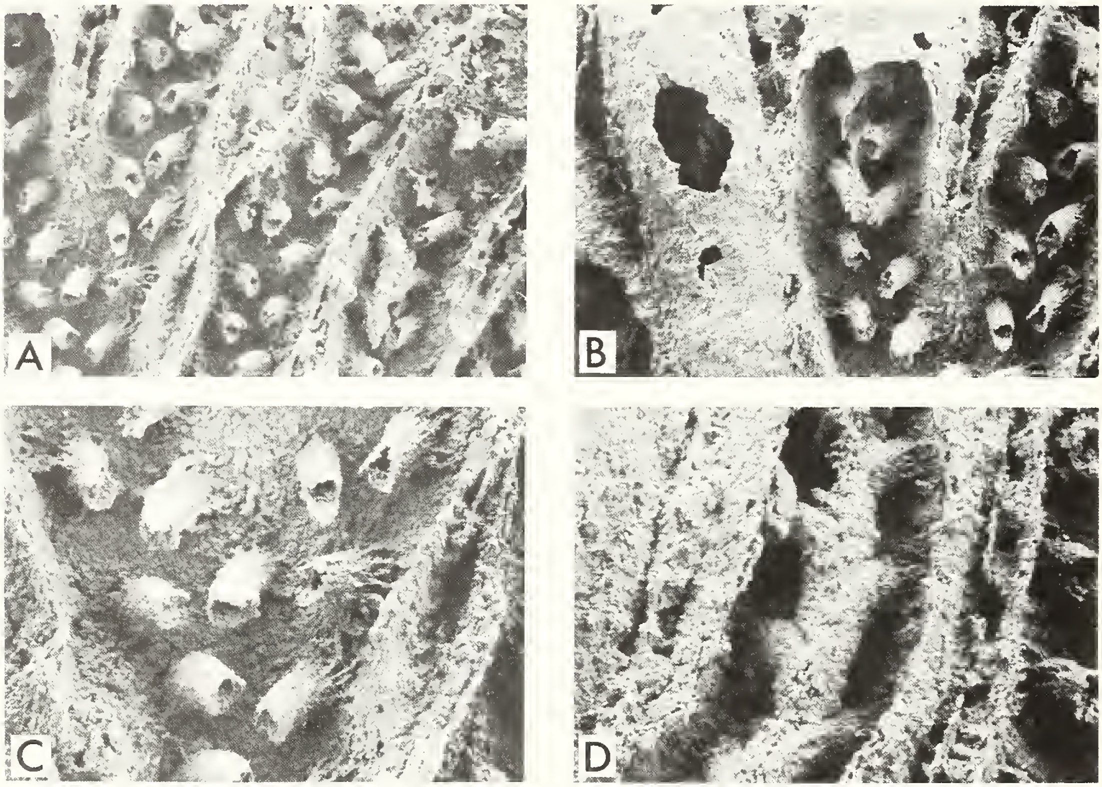


TEXT-FIG. 3. Outline shapes of some branching fragments of *Alwynopora orodamnus* sp. nov. Arrows indicate growth direction; + indicates a branch growing towards the observer. *a*, BM(NH) PD6263; *b*, PD6241; *c*, PD6266; *d*, PD6238; *e*, PD6251; *f*, PD6265.

Zooecial apertures are circular to elliptical in shape and elongated transversely, longitudinally, or obliquely. This apparently depends on preservational factors, several branches showing indications of compression and/or shear. A variably thick rim surrounds each aperture and measurements of apertural width varying between 0·08 and 0·22 mm are similarly dependent on state of preservation. Occlusion of apertures is a characteristic of some branches; this may be due to diaphragm formation or an artefact of silicification. Zooecial chambers are moderately long and have a length that slightly exceeds external interapertural spacing. In shape they are essentially tubular, tapering towards the locus of budding on the midline near the reverse side of the branch. Zooecia were budded alternately left and right of the branch midline, paralleled the branch axis initially, and then turned outwards to meet the colony surface more or less at right angles. Diaphragms and other intrazooecial partitions have not been observed.

Affinities. Delicately branched Ordovician bryozoans exist among three orders, Cyclostomata, Cryptostomata, and Fenestrata. All Ordovician cyclostomes are single-walled stenolaemates *sensu* Borg (1926). These include branching species of *Clonopora* Hall, 1883, *Kukersella* Toots, 1952, *Mitoclema* Ulrich, 1882, *Mitoclemella* Bassler, 1952, and *Wolinella* Dzik, 1981. Here the calcified zooid frontal wall that forms the branch surface is an exterior wall incapable of adding more calcite to its outer surface. Therefore proximally thickening branches of the kind found in *A. orodamnus* cannot be produced. However, cryptostomes and fenestrates are double-walled stenolaemates with calcified zooid frontal walls that are interior walls and were capable of adding calcification to their outer surfaces. *A. orodamnus* clearly belongs to one of these groups. Among Ordovician genera, only arthrostylid cryptostomes (e.g. *Nematopora* Ulrich, 1888) and the fenestrate genus *Enallopora* d'Orbigny, 1849 closely resemble *A. orodamnus*. However, branches of arthrostylids tend to be straighter and do not develop the same amount of proximal thickening as *A. orodamnus*. Furthermore, *A. orodamnus* shows no indications of the uncalcified articulations found in most arthrostylids. The affinities of *Alwynopora* with the Order Fenestrata are indicated by a combination of three features: restriction of zooecial apertures to one side only of the branches, unjointed branches, and proximally thickened branches.

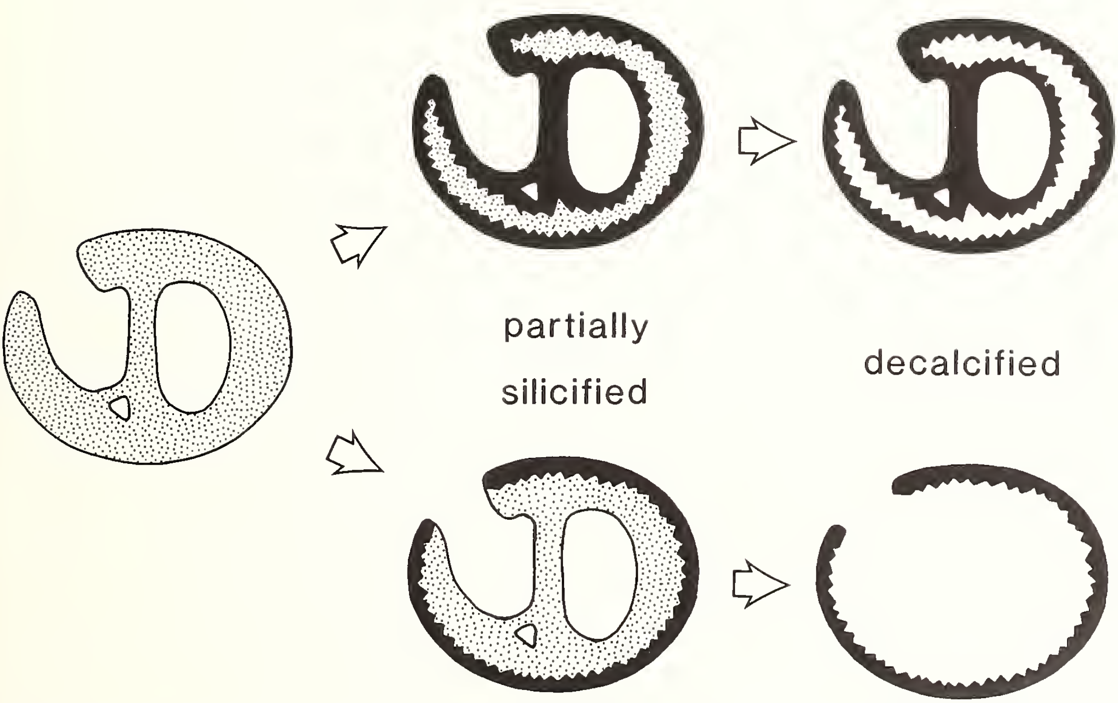
Enallopora, together with its subjective junior synonym *Protocrisina* Ulrich, 1889, has a branching pattern like that of *A. orodamnus* but the branches bear three or four rows of zooecial apertures, often with small 'accessory pores' between them. Elsewhere in the Order Fenestrata different generic names are accorded to taxa having two and more than two rows of zooecial apertures. These may reflect important differences in budding pattern. Therefore, distinction between *Enallopora* and *Alwynopora* is justified, although a close relationship between the two genera seems likely. Some species of *Enallopora*, such as *E. oeilensis* (Wiman, 1902) from the Ashgill of Sweden, exhibit proximal branch thickening of a similar magnitude to *A. orodamnus* (see Brood 1982, fig. 7A and F). *Enallopora* is unusual among fenestrates in lacking styles within the laminated skeleton (F. K. McKinney,



TEXT-FIG. 4. *Alwynopora orodamnus* sp. nov., thick proximal branches with silicification of internal structure, BM(NH) PD6272. Scanning electron micrographs of reverse surface of uncoated specimen using back-scattered electrons. A, closely spaced branches with basal walls removed and silicification of distal parts of zooecial linings, × 14; B, branches with basal walls intact (left) and removed, × 16; C, detail of silicification of distal parts of zooecial linings, × 28; D, complete silicification of zooecial linings showing zooecia arising from a budding locus at the centre of the branch, × 31.

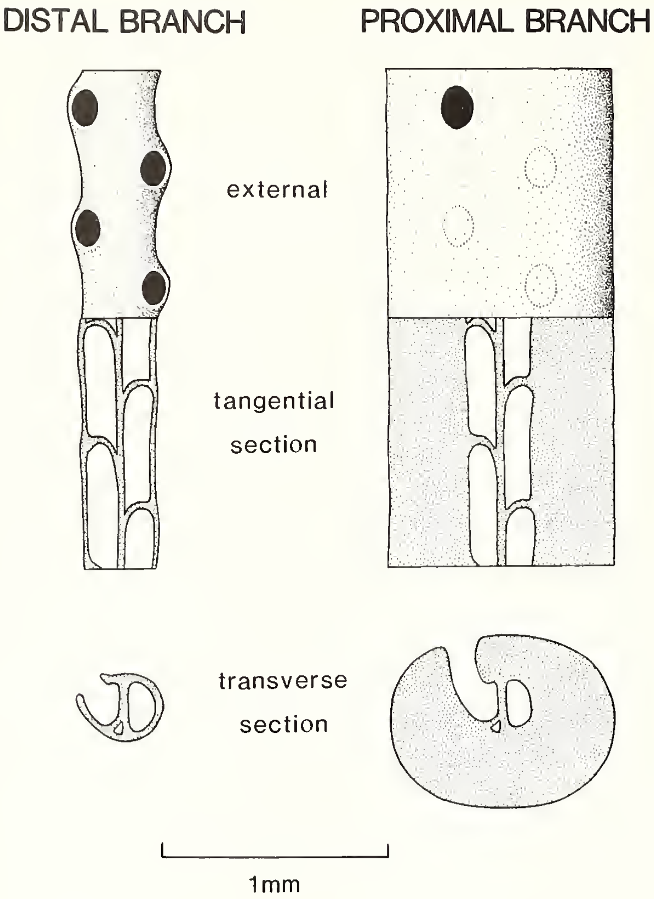
pers. comm.). Unfortunately, unsilicified material of *Alwynopora* is not available for comparison of wall microstructure. Though *Enallopora* is usually assigned to the Family Fenestellidae King, 1850 (see Bassler 1953), the atypical microstructure may justify revival of the Family Enalloporidae Miller, 1889 to which *Alwynopora* is also tentatively assigned.

Discussion. The silicified preservation of *A. orodamnus* necessitates some interpretation as a preliminary to reconstruction of original skeletal morphology. In some specimens only the outer surfaces of the branches have been silicified so that acid treatment leaves specimens as hollow tubes lacking internal structure (text-fig. 5). Tavener-Smith (1973) reported similar preservation of Carboniferous fenestrates where silicification evidently progressed from the outside of the branches inward. In other specimens of *A. orodamnus*, however, silicification is more extensive and includes zooecial linings. The void between these linings and the outer branch surface represents unsilicified skeleton (text-fig. 5). These specimens are valuable in revealing details of internal structure including zooecial shape, dimensions, and budding pattern.



TEXT-FIG. 5. Interpretation of silicification in *Alwynopora orodamnus* sp. nov. shown in transverse section. Calcified parts are stippled, silicified parts are black. Silicification occurs as a rind replacing the outer surface layers of skeleton and sometimes (upper sequence) the lining of the zooecial chambers.

The high degree of variability in branch thickness between specimens of *A. orodamnus* also warrants comment. Variation is continuous and there is no indication that more than one species is present at Tourmakeady. Thin and thick branches have the same alternating biserial arrangement of apertures with equivalent interapertural spacing. A gentle but distinct distal taper in some branch lengths (e.g. text-fig. 3*c*) is evidence that branch thickness is age-related. Young branches are narrow and have thin walls and sinuous margins (e.g. text-fig. 2c). During growth addition of calcification to the outer surfaces of branches resulted in substantial branch thickening and loss of sinuosity (text-fig. 4). This was accompanied by lengthening of zooecial chambers, divergence of apertures



TEXT-FIG. 6. Diagrammatic reconstruction of morphology in a distal branch (young) and a proximal branch (old) of *Alwynopora orodamnus* sp. nov. Calcified wall is evenly stippled in the tangential and transverse sections.

from the branch midline, and by the formation of diaphragms over zooecial apertures (assuming aperture occlusion is not a preservational artefact).

An important consequence of branch thickening was the reduction and eventual elimination of the spaces between adjacent branches (e.g. text-fig. 4). As fenestrate bryozoans are thought to have generated feeding currents that drew water towards the frontal surface of branches and expelled filtered water through the spaces between branches and towards their reverse surface (Cowen and Rider 1972; Taylor 1979), occlusion of the spaces between branches during colony growth may have impaired feeding. However, basal regions of bryozoan colonies (e.g. adeoniform cheilostomes, see Cheetham and Thomsen 1981) may be occupied by zooids which have lost their feeding function. The same is likely for *A. orodamnus* colonies, especially if zooecial apertures in basal branches were closed by diaphragms. Basal branches of *A. orodamnus* may have fulfilled a supportive function. For this role the kind of thick calcification present in many colonies would have been advantageous in resisting bending stresses imposed by water movement around the colony (cf. adeoniform cheilostomes, see Cheetham and Thomsen 1981).

LOWER ORDOVICIAN BRYOZOA

Discovery of the first fenestrate bryozoan in the lower Ordovician prompts a brief review of world-wide records of lower Ordovician Bryozoa. As yet there are no unequivocal bryozoans of pre-Arenig age (Taylor 1984), but by the late early Ordovician a moderately diverse bryozoan fauna had become established. Table 1 summarizes the bryozoan taxa recorded from the lower Ordovician with their stratigraphical occurrence and provenance. This table is the basis for the following comments on taxonomic distribution, morphological diversity, and palaeogeographical distribution. The lower–middle Ordovician boundary is here placed at the top of the Arenig Series in Britain (Williams *et al.* 1972), very approximately equivalent to the top of the Volkhov Stage (B2) in Estonia, and the top of the Valhallen Stage in North America (Fortey 1980).

Taxonomic distribution

A striking feature of the thirty-eight species recorded from the lower Ordovician is their wide taxonomic distribution (Table 1). All five orders of stenolaemate bryozoans recognized in the revised bryozoan *Treatise* (Boardman *et al.* 1983) are represented. Given the uncertainties in correlation within the lower Ordovician, one may conclude that stratigraphical evidence on the relative time of appearance of the orders is never likely to be of value in resolving phylogenetic relationships at ordinal level. A smaller proportion of taxa have lower Ordovician representatives at successively lower taxonomic levels. Three of twelve (25%) cystoporate families (Utgaard *in* Boardman *et al.* 1983) are known from the lower Ordovician, eight of nineteen (42%) trepostome families (Astrova 1978, with the addition of the Dianulitidae), and two of thirteen (15%) cryptostome families (Karklins *in* Boardman *et al.* 1983; Blake *in* Boardman *et al.* 1983); lack of up-to-date information on fenestrate and cyclostome classification precludes their analysis. At the genus level the lower Ordovician has only four of ninety (4%) cystoporate genera, eleven of eighty-seven (13%) trepostome genera, and three of eighty (4%) cryptostome genera. Such early diversification at high taxonomic levels is also a feature of many phyla other than the Bryozoa. However, unlike some phyla (notably the Echinodermata, see Paul 1979) many of the higher taxa established during early bryozoan evolution were of long duration. All five stenolaemate orders persisted throughout the Palaeozoic at least.

Another aspect of the data (Table 1) is the considerable contribution of trepostomes to the early diversification of the Bryozoa. This early trepostome dominance was eroded somewhat during the middle Ordovician when other orders, especially the Cryptostomata (e.g. Ross 1964), became more important. However, palaeogeographical distribution may be a major factor in this apparent evolutionary pattern. Most lower Ordovician bryozoans come from the trepostome-dominated region of Estonia whereas younger faunas are known also from regions of markedly different faunal composition, e.g. the middle to upper Ordovician of the Siberian Platform where trepostomes are scarce and ptilodictyine cryptostomes dominate (Nekhoroshev 1961).

Morphological diversity

Lawood and Taylor (1979) have already emphasized the wide variety of colony-forms present in bryozoans of the Ordovician as a whole and their possible ecological significance. Many of these colony-forms were established during early Ordovician times. Dome-shaped colonies (e.g. *Revalotrypa gibbosa*) are particularly prevalent but also present in the lower Ordovician are cylindrical branched colonies of several types (e.g. *Wolinella baltica*, *A. orodamnus*, *Dittopora annulata*), frondose colonies (e.g. *Trepocryptopora dichotomata*), and laminate colonies (e.g. *Ceramopora*? *unapensis*). Subdivision of colonies into subcolonies (cormidia) is known from lower Ordovician bryozoans, notably *Dianulites hexaporites* and the dianulitid described by McLeod (1978). Other morphological characters (many used taxonomically) include laminar and granular wall structures, acanthostyles, interzooidal communication pores, diaphragms, hemiphragms, interzooidal vesicles, lunaria, calcified exterior walls, and various types of zooidal polymorph. An analysis of the distribution of these and other characters would clearly be of value in resolving phylogenetic relationships. Lower Ordovician representatives of each stenolaemate order may be expected to possess a high proportion of morphological characters in primitive states. This could assist the distinction between primitive and advanced character states which is important in reconstructing phylogeny within each stenolaemate order.

TABLE 1. Records of bryozoans from the lower Ordovician

Taxon	Stratigraphy	Locality	Reference
Order Cyclostomata			
Family Corynotrypidae			
Wolinella baltica Dzik	M. Volkhov Stage	Estonia; Poland	Dzik 1981
Order Cystoporata			
Family Ceramoporidae			
Ceramopora? *unapensis* Ross	Kindblade Fm.	Oklahoma	Ross 1966
Family Anolotichiidae			
Lamtshinopora hirsuta Astrova		Vaigach Is., U.S.S.R.	Astrova 1965; Utgaard in Boardman *et al.* 1983
Profistulipora arctica Astrova		Novaya Zemlya, U.S.S.R.	Astrova 1965; Utgaard in Boardman *et al.* 1983
Profistulipora retrusa Astrova		Novaya Zemlya, U.S.S.R.	Astrova 1965; Utgaard in Boardman *et al.* 1983
Family Xenotrypidae			
Xenotrypa primaeva (Bassler)	Volkhov Stage	Estonia	Bassler 1911; Utgaard in Boardman *et al.* 1983
Order Trepostomata			
Family Esthonioporidae			
Esthoniopora communis Bassler	Volkhov Stage	Estonia	Bassler 1911; Mannil 1959
Esthoniopora lessnikovae (Modz.)	Volkhov Stage	Estonia	Modzalevskaya 1953; Mannil 1959
Esthoniopora curvata Bassler	Volkhov Stage	Estonia	Mannil 1959
Family Orbiporidae			
Orbipora solida Bassler	Volkhov Stage	Estonia	Modzalevskaya 1959
Orbipora acanthopora Bassler	Volkhov Stage	Estonia	Modzalevskaya 1953
Family Dittoporidae			
Dittopora clavaeformis Dybowski	Volkhov Stage	Estonia	Bassler 1911; Mannil 1959
Dittopora annulata (Eichwald)	Volkhov Stage	Estonia	Bassler 1911; Modzalevskaya 1953
Dittopora ramosa Modzalevskaya	Volkhov Stage	Estonia	Modzalevskaya 1953
Dittopora sokolori Modzalevskaya	Volkhov Stage	Estonia	Modzalevskaya 1953
Hemiphragma rotundatum Bassler	Volkhov Stage	Estonia	Modzelevskaya 1953
Family Halloporidae			
Diplotrypa petropolitana Nicholson	Volkhov Stage	Estonia	Bassler 1911
Diplotrypa bicornis (Eichwald)	Volkhov Stage	Estonia	Bassler 1911
Family Trematoporidae			
Revalotrypa gibbosa (Bassler)	Volkhov Stage	Estonia	Bassler 1911; Mannil 1959
Nicholsonella huoi Yang	U. lower Ord.	Liangshan, China	Yang 1957
Nicholsonella papillaris Modz.	Volkhov Stage	Estonia	Modzalevskaya 1953
Nicholsonella rotundicellularis Modz.	Volkhov Stage	Estonia	Modzalevskaya 1953
Nicholsonella arborea Modz.	Volkhov Stage	Estonia	Modzalevskaya 1953
Family Amplexoporidae			
Anaphragma vetustum Bassler	Volkhov Stage	Estonia	Modzalevskaya 1953
Monotrypa helenae Modzalevskaya	Volkhov Stage	Estonia	Modzalevskaya 1953
Family Atactotoechidae			
Orbignyella antiqua Modzalevskaya	Volkhov Stage	Estonia	Modzalevskaya 1953
Family Dianulitidae			
Dianulites fastigiatus Eichwald	Volkhov Stage	Estonia	Bassler 1911
Dianulites petropolitana Dybowski	Volkhov Stage	Estonia	Bassler 1911; Modzalevskaya 1953
Dianulites glauconiticus Mannil	Volkhov Stage	Estonia	Mannil 1959
Dianulites janischewskyi Modz.	Volkhov Stage	Estonia	Modzalevskaya 1953
Dianulites hexaporites (Pander)	Volkhov Stage	Estonia	Modzalevskaya 1953
Dianulites multimesoporicus Modz.	Volkhov Stage	Estonia	Modzelevskaya 1953
'Dianulitid'	Cassinian	Arkansas; Missouri	McLeod 1978
Order Cryptostomata			
Family Arthrostylidae			
Arthroclema cf. *armatum* Ulrich	Volkhov Stage	Estonia	Bassler 1911; Mannil 1959
Family Stictoporellidae			
Stictoporellina gracilis (Eichwald)	Volkhov Stage	Estonia	Bassler 1911; Mannil 1959
Family incertae sedis			
Trepocryptopora dichotomata Yang	U. lower Ord.	Liangshan, China	Yang 1957; Karklins in Boardman *et al.* 1983
Trepocryptopora flabelata Yang	U. lower Ord.	Liangshan, China	Yang 1957
Order Fenestrata			
? Family Enalloporidae			
Alwynopora orodamnus sp. nov.	U. Arenig	Tourmakeady, Eire	this paper

Palaeogeographical distribution

Lower Ordovician bryozoans are known from three main palaeogeographical regions: the Baltic Plate (Estonia and Novaya Zemlya), the North American Plate (Tourmakeady and localities in the U.S.A.), and the Yangtze Plate (Liangshan). During Arenig times the Baltic Plate is likely to have been temperate (Cocks and Fortey 1982), the North American Plate tropical (Scotese *et al.* 1979), and the Yangtze Plate tropical or subtropical (R. A. Fortey, pers. comm. 1983). These three plates were widely separated, demonstrating the wide distribution of bryozoans in the early Ordovician. This substantial geographical spread in conjunction with the taxonomic variety of Arenig bryozoans points to a considerable pre-Arenig history that is as yet unknown and may be crucial to the testing of various models (e.g. Larwood and Taylor 1979; Taylor 1981) of early bryozoan diversification.

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NEW LATE DEVONIAN GENERA AND SPECIES OF TORNOCERATID GONIATITES

by M. R. HOUSE *and* J. D. PRICE

ABSTRACT. A brief review is given of the evolutionary relationships of generic groups in the Devonian goniatite family Tornoceratidae (Ammonoidea) as an introduction to the description of two new genera, *Falcitornoceras* and *Crassotornoceras*, from levels around the Frasnian–Famennian boundary. Species and subspecies of these genera are described from western Europe and *Crassotornoceras* is recorded also from North America. A detailed sequence of faunas with *Falcitornoceras* is described from the Montagne Noire across the Frasnian–Famennian boundary. Statistical data regarding the ontogeny of both genera are provided and a description is given of the early stages of *Falcitornoceras* which demonstrates the marked change in ornament at the end of the ammonitella stage, of the type already known in other members of the family. The following new species and subspecies are described: *C. annissi*, *F. falciculum falciculum*, *F. falciculum constrictum*, and *F. falciculum wagneri*.

EUROPEAN tornoceratids have never been the subject of thorough systematic study and new genera and species have been described in a rather random way over the last 150 years. This paper is primarily concerned with poorly known forms which appear to have some biostratigraphical usefulness around the Frasnian–Famennian boundary. The material described is wholly from western Europe, particularly from the Rhenish Schiefergebirge, Brittany, the Montagne Noire, and central Spain. As an introduction it is thought appropriate to outline something of views on the evolution of the Tornoceratidae as a whole since, apart from a popular account (House 1963*a*), there is no up-to-date review of the matter. This will serve to highlight some of the problems associated with the derivation of the new forms described. It is convenient at this stage, and pending a thorough revision, to use some generic groupings in a rather informal way, the purpose being to draw attention to species groups rather than to name them prematurely. Reference in the text is made to both ammonoid and conodont zones (text-fig. 1); correlation between the two schemes is based largely on Ziegler (1979).

EVOLUTION OF THE TORNOCERATIDAE

A generalized interpretation of the time distribution and morphological groups within the Tornoceratidae is given in text-fig. 1. The group is extremely common internationally in the Givetian and Frasnian but gradually declines in importance through the Famennian, the last record being representatives from the Wocklumeria Stufe referred by authors to *Lobotornoceras* (Pfeiffer 1954; Petter 1959; Korn 1981; Weyer 1981). A modestly wide range of shell form is represented in the family which is characterized by a distinctive sutural pattern comprising a ventral lobe, usually small and V-shaped, an adult lateral lobe which arises during early ontogeny on a highly arched lateral saddle, and a deeply V-shaped mid-dorsal lobe. Within the family certain genera have slightly more complex sutures, as outlined in the discussion below. In terms of the Russian nomenclature, the divergence from the basic VLUD pattern may be expressed as follows—$VLU_1:U_1D_1$ to $V(L_1)LUD$ to LUD to V(L)(U)D. Growth lines are almost invariably biconvex after a convex form in the ammonitella (House 1965). American tornoceratids have been monographed (House 1965); these faunas generally lack diversity in comparison with European forms, but recent finds have widened the representation known (House 1978; Kirchgasser and House 1981). Rare tornoceratids occur in South America (Leanza 1968; Hünicken *et al.* 1980). A thorough review of Russian records

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(Bogoslovskiy 1971) unfortunately gives little emphasis to precise biostratigraphic discrimination of the faunas.

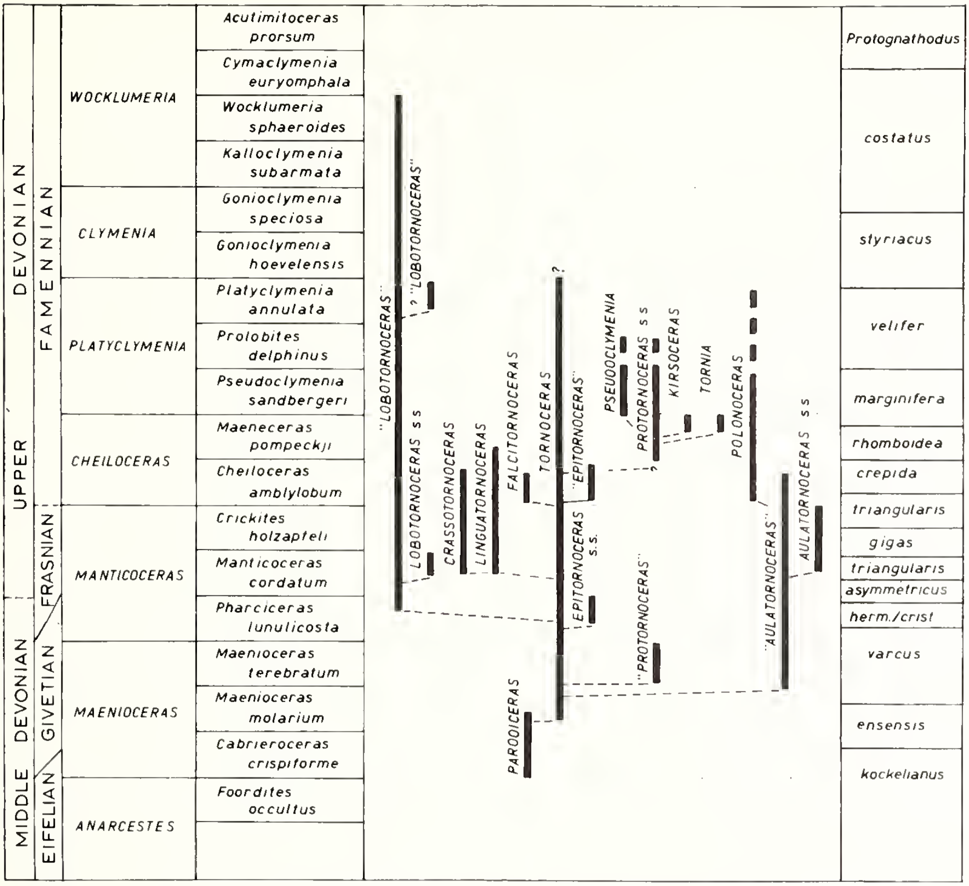
The earliest genus referred to the family is *Parodiceras*, which is thought to have arisen from Eifelian anarcestids, but no precise source has been identified. The genus *Parodiceras* seems to commence in the late Eifelian of current definition. The earliest European records appear to be from the Oderhausen Kalk in the Rhenish Schiefergebirge, probably from the conodont *kockelianus* Zone. In North America, the earliest occurrence is in the Werneroceras Bed of New York State which is placed by Klapper (1981) also in the *kokelianus* Zone, equivalent to levels in the Junkerberg Beds of the Eifel and upper Couvinian (Co2C, R/IV) of Belgium. The sutural form of *Parodiceras* shows only an incipient development of the lateral lobe which characterizes later members of the family. This fact led Petter (1959) to place the genus uniquely in a separate family, the Parodiceratidae, but this has not been generally accepted.

Tornoceras, the longest ranging member of the family, is thought to have been derived from *Parodiceras* by the acquisition of a well-developed lateral lobe; it shows biconvex growth lines but these may approach convexity in the outermost parts of the body chamber. In New York State, *Tornoceras* first appears in the Marcellus Formation, a level thought to correlate with the *ensensis* Zone (Klapper 1981). The genus is widespread in the Givetian. In the late Eifelian and Givetian, the Tornoceratidae are often accompanied by an unrelated but homoeomorphic group, including *Foordites* and *Holzapfeloceras* which Petter (1955) showed to have quite a different ontogeny, but that group becomes extinct in the early *varcus* Zone.

No detailed work to modern standards has been done on European *Tornoceras*. The commonest form referred here is *T. simplex* (von Buch, 1832, p. 42, pl. 2, fig. 7), the holograph of which is a virtually uninterpretable thumb-nail sketch which might even be a *Foordites* or *Holzapfeloceras*. The type material has not been located and until it is, or a neotype chosen, and a thorough description of it published, the name has little value. The convention has been to base the species on figures such as that of Wedekind (1917, pl. 16, fig. 12). Used in this sense, the similarity and probable synonymy between this species and *T. uniangulare* (Conrad), the type species of the genus, has generally been conceded. The precise time level of the type material of *T. uniangulare* is not clear. It comes from the Leicester Pyrite (or Marcasite) in New York State (House 1965), which represents a *remanié* bed (Huddle and Repetski 1981) derived from levels earlier than the upper *hermanni-cristatus* to lower *asymmetricus* Zone date given by conodonts (Klapper 1981), probably from an horizon immediately overlying the Leicester Pyrite. Hence the assertion that the true *T. uniangulare* is pre-Tully in age (House 1965) may be true, but it is not proven, nor likely to be. *Tornoceras* is common in the Frasnian and is very widely distributed but declines in significance in Famennian faunas. The last clear records are probably high in the Platyclymenia Stufe (Sobolev 1912; Dybczyński 1913).

A distinctive group of more stratigraphical significance is represented by *Linguatornoceras* House, 1965, in which the shell form is well-rounded rather than flattened laterally, and the lateral lobe is small, narrow, and tongue-shaped. It occurs from the mid Manticoceras Stufe to top Cheiloceras Stufe (*cordatum* to *pompeckji* Zones in ammonoid terms). Whether *Linguatornoceras* should be regarded as a separate genus, as a subgenus of *Tornoceras*, or synonymized with *Tornoceras* is a matter of varied current opinion. Its distinctiveness and stratigraphical value, however, cannot be disputed and on those grounds is kept separate here. *Tornoceras* and *Linguatornoceras* represent conservative stocks from which other genera may be derived by modification of the shell form and often additionally by changes in the sutural ontogeny. *Linguatornoceras* at present seems the most likely ancestor of *Cheiloceras* and the Cheiloceratidae by the adoption of convex growth lines, a modification already seen in the outer whorls of some Frasnian specimens.

Distinctive derivatives of *Tornoceras* are represented by *Lobotornoceras* in which a small saddle is added on the umbilical seam, and the umbilical lobe moves on to the flanks. The true *Lobotornoceras*, type species *L. ausavense* (Steininger, 1853, neotype designated by House 1978, pl. 9, figs. 8, 14), is only known with certainty from the upper *cordatum* Zone associated with a typical fauna of the Büdesheimer Schiefer at Büdesheim, West Germany. This species comprises a laterally compressed goniatite with about five prominent constrictions per whorl. Two other quite distinctive groups have



TEXT-FIG. 1. Supposed evolutionary relationships within the Tornoceratidae. The use of taxonomic names is described in the text. Note that the *amblylobum* Zone is sometimes termed the *curvispina* Zone. Correlation of ammonoid zones with conodont zones is based largely on Ziegler (1979).

been included within *Lobotornoceras*. The one marked as '*Lobotornoceras*' on text-fig. 1 has a stouter whorl form and no constrictions; the earliest record of this is from around the *lunulicosta*/*cordatum* Zone boundary in a fauna from Virginia (House 1978, p. 59) and it also occurs in New York State (Kirchgasser and House 1981). There is then a gap in the record, and a number of similar forms have been described from the early Famennian which include probably all of the Famennian records of *Manticoceras*, i.e. *M. superstes* Wedekind, *M. nehdense* Lange, and *M. niedzwiedzkii* (Dybczyński), as was suggested by Clausen (1968*a*) and Jux and Krath (1974). The only remaining records of *Manticoceras* from the Famennian are one specimen found loose at La Serre with the typical *Cheiloceras* fauna, and which now appears to be a case of contamination, and the record of a specimen from the *crepida* Zone of Sessacker (Ziegler 1962) which should be disregarded until convincing illustrations or descriptions of it are given to justify the determination. Later in the Famennian there are few records of *Lobotornoceras* until the last in the Wocklumeria Stufe (Weyer 1981, p. 5) which is associated with a fauna suggestive of the *paradoxa* Zone. Finally, there is the group marked as ?'*Lobotornoceras*' on text-fig. 1, in which ventrolateral furrows occur additionally. This is represented only by one record of *L.* (?) *bicaniculatum* (Petter 1959) from North Africa, and the recognition of a similar form in Kazakhstan by Bogoslovskiy (1971). This group might equally well be developed from '*Aulatornoceras*' by sutural elaboration but intermediate forms are not recorded from the intervening *sandbergeri* and *delphinus* Zones.

Oxyconic tornoceratids have usually been referred to *Epitornoceras* although, as pointed out by House (1978, p. 60), the type species *E. mithracoides* (Frech) is trochoidal in form rather than oxyconic; the types are recorded as having come from the *lunulicosta* Zone at Eibach, West Germany. The sharply oxyconic species *E. peracutum* (Hall) from New York is from the upper part of the same zone. Both species will belong to the late Givetian if current proposals of the Devonian Subcommission are accepted. There is then a gap in the record and oxyconic forms of rather similar appearance occur in the Cheiloceras Stufe. In Poland, Dr. H. Makowski has demonstrated (to M.R.H.) that all gradations occur from typical *Tornoceras* to these oxyconic forms among faunas wholly from the Cheiloceras Stufe, indicating a contemporary derivation. The Famennian oxycones must therefore be phylogenetically distinct from and independent of the earlier group (or rather this is the simplest explanation to be accepted for the present as most probable). No new generic name is proposed for this group here but it is marked as '*Epitornoceras*' on text-fig. 1. The *Epitornoceras* recorded from the Cheiloceras Stufe of Western Australia by Petersen (1975) belongs here.

Widely umbilicate tornoceratids with the simple whorl section of *Tornoceras* are referred to *Protornoceras*. The earliest is '*P.*' *foxi* House from the Givetian of Cornwall. There is then a long gap in the record; from the Cheiloceras Stufe, and slightly later, some twenty-five specific names have been proposed for tornoceratids of this type. Since the type species of *Protornoceras*, *P. polonicum* Dybczyński from the early Famennian of Kielce, Poland, is part of this latter group, it is the '*P.*' *foxi* group which must be renamed should it come to be proven that they are independently derived. There appear to be no confirmed records of *Protornoceras* higher than the *delphinus* Zone, or the *marginifera* Zone of the conodont terminology. The genus *Pernoceras* Schindewolf (1922, p. 188; 1923, p. 310) is best regarded as a synonym of *Protornoceras* but the type species of the former, *Protornoceras kochi*, shows a tabular venter and flattened sides as well as an open umbilicus and therefore approaches the group marked as '*Aulatornoceras*' on text-fig. 1.

Two genera are thought to be derived from more typical *Protornoceras* by simplification of the suture and slight changes in the shell form. In *Kirsoceras* (Bogoslovskiy 1971) the ventral lobe is lost, the lateral lobe is relatively increased in size, and the latero-umbilical lobe decreased in prominence significantly; this genus is only known from the Cheiloceras Stufe (presumably late) of the Urals. In *Tornia* House, 1970, probably from the *pompeckji* Zone of Kielce, Poland, the suture passes across the flanks from the ventral lobe with only the barest trace of a lateral or umbilical lobe. These two genera have a striking resemblance to some of the earliest clymeniids, notably in the shell form, the ventral suture, the shape of the septum, and especially the deep narrow median dorsal lobe appropriately similar to that carrying the siphuncle in the clymeniids. Schindewolf (1972) followed by Bogoslovskiy (1976) have both not accepted the view of House (1970) that this group might form the initiation point for the Clymeniida. Schindewolf preferred his own earlier hypothesis of an ancestor in *Archoceras*, arguing that the lateral lobe in the clymeniids arises from an umbilical position in early ontogeny, whereas in the tornoceratids it arises adventitiously on an arched early saddle. But this is not in dispute. The early stages of *Tornia* are not known but the point is that, judging from the early stages of other tornoceratids, with an almost non-existent adult lateral lobe *Tornia* will be very unlikely to have an adventitious lobe in the early stages at all. It is in the early stages where dorsal migration of the siphuncle occurs and where consequent modification of the sutural pattern is to be expected. Neither Schindewolf (1972) nor Bogoslovskiy (1976) addressed this problem, nor did they comment on the fact that the whole geometry of the tornoceratid septum matches that of the clymeniids, whilst the archoceratid septum (the alternative point of origin) is fundamentally unlike it. Unfortunately, so little work has been done on the early stages of all these forms that a speedy resolution of the problem seems unlikely.

Quite bizarre derivatives, presumably from *Protornoceras*, are those which develop a sigmoidally shaped lateral lobe and often an incipient lobe on the ventrolateral saddle, an overall pattern resembling that of the clymeniid *Cymaclymenia*, hence their name *Pseudoclymenia* Frech, 1897. The type species is *Pseudoclymenia sandbergeri* after which is named the zone in which the group reaches its acme, although it occurs also in the overlying *delphinus* Zone. Many of the species of this genus have been reviewed by Bogoslovskiy (1971). Some species are almost serpenticonic in form.

Forms of tornoceratid in which ventrolateral furrows or grooves and often festoon-like constrictions and lirae occur are generally referred to *Aulatornoceras* Schindewolf, 1922. The evolution of this group is complex and virtually nothing has been done to try to sort out the various strands involved. The type species is *A. auris* (Quenstedt, 1846), the types of which have apparently been lost (there is no trace of them with Quenstedt's other material at Tübingen); they came from the Büdesheimer Schiefer and hence almost certainly from the upper *cordatum* Zone. A variety of forms, smooth to ribbed and open to closed umbilicate, have been referred to the species. In the interests of nomenclatorial clarity a neotype is here selected (Pl. 17, figs. 1–4) from the type locality. This species forms one of a group of essentially Frasnian forms which are quite heavily sculptured and which possess, to a greater or lesser extent, an open umbilicus. By contrast, there are laterally compressed, closed umbilicate forms with weakly developed ornament, but with ventrolateral furrows, which are known patchily from the late Givetian (House 1963*b*) to levels in the early Famennian; these are marked as '*Aulatornoceras*' on text-fig. 1. It has always been tempting to consider this group as making a dimorphic pair with *Tornoceras*. Ontogenetic comparison, however, gives as yet no evidence to support this view. Alternatively, an independent origin from *Tornoceras* of ventrolaterally furrowed forms on several occasions seems more probable but direct links have not been established.

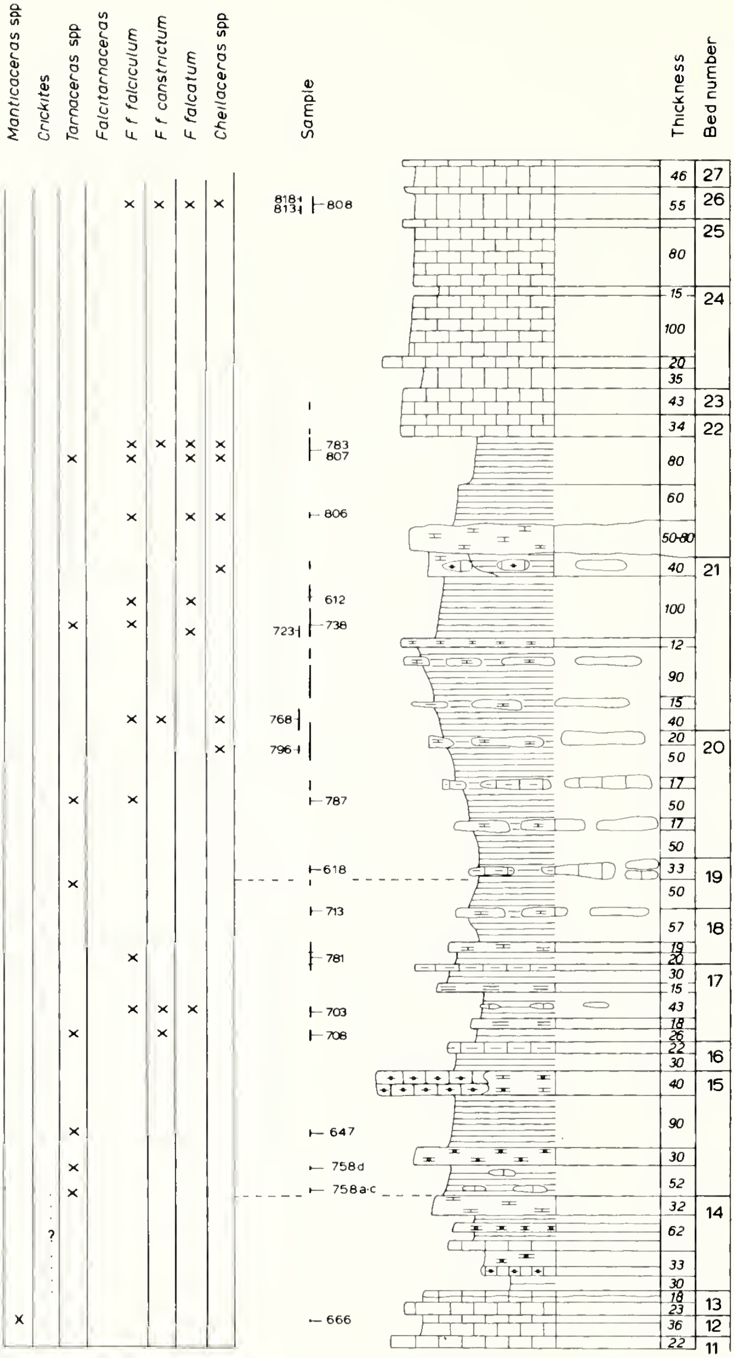
It is from the long-ranging group '*Aulatornoceras*' that *Polonoceras* (Dybczyński 1913) may have been derived by the development of slight ribbing (in some) and a discoidal form with tabular venter. Some might consider *Polonoceras* and '*Aulatornoceras*' as synonyms. If so, the former name should be used. The type species, by the designation of Miller (1938, p. 142), is *P. planum* Dybczyński, a species which was illustrated as showing a sharp angular bend in the suture from the crest of the latero-umbilical saddle to the lateral lobe; this illustration has been widely copied but the accompanying photographic illustration does not show this feature. The type came from the now defunct Sieclucki Brickpit in Kielce, and Dr. Makowski has informed one of us that the site is now the roundabout in Kielce at the junction of Al Lenina and Bohaterow Warszawy. In the absence of either evidence of the original material, or satisfactory figures on which to base the genus, a topotype is illustrated here (Pl. 17, figs. 8–10) which may serve as a better indication of the species. Forms referred to *Polonoceras* occur in the *amblylobum* Zone at La Serre, Montagne Noire, and also at Beil, Germany. It is possible that the type material was from the *pompeckji* Zone.

Finally, there are the two groups here distinguished at generic level. *Crassotornoceras* gen. nov. is named for a group of micromorphic rotund tornoceratids with periodic constrictions in the inner and often outer whorls. This genus is known from the upper *cordatum* Zone, is common in the *holzapfeli* Zone, and is known from the earliest Famennian at Nehden; it was probably derived from *Linguatornoceras*. *Falcitornoceras* gen. nov. is characterized by spectacularly close-set ribbing on the early whorls of a type not known elsewhere in the family and, indeed, unmatched in any Devonian ammonoid. These are best known only from the Cheiloceras Stufe, but they occur also before the entry of *Cheiloceras* in the section at La Serre in the Montagne Noire (text-fig. 2); whether they occur in the Frasnian will depend on how the base of the Famennian comes to be defined.

SYSTEMATIC PALAEONTOLOGY

Dimensions. All dimensions are in millimetres unless otherwise stated. Shell form parameters are abbreviated as follows: D, diameter; WW, maximum whorl width at the stated diameter; WH, projection of distance between venter and umbilical wall or shoulder, whichever is the greater, in the plane of the spiral; UW, distance between the umbilical wall, shoulder, or seam at the stated diameter and at precisely half a whorl previously, whichever is the least; Ribs, number of ribs in the whorl preceding the maximum diameter.

Repositories of specimens. BerlM, Museum für Naturkunde, East Berlin; BM(NH), British Museum (Natural History), London; IG, Institute Géologique, Université de Louvain, Belgium; LPB, Laboratoire de


Manticoceras spp
Crickites
Tornoceras spp
Falcitornoceras
F f falciculum
F f constrictum
F falcatum
Cheiloceras spp
Sample
Thickness
Bed number
818
813
808
783
807
806
612
723
738
768
796
787
618
713
781
703
708
647
758d
758a-c
666
?
46
55
80
15
100
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50-80
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TEXT-FIG. 2. Section through the uppermost Frasnian and lowermost Famennian in Trench C (text-fig. 9), around 600 m east of La Roquette, La Serre, south of Cabrières, Hérault, Montagne Noire, France, showing the levels from which goniatites have been obtained. Bed thickness in cm. Symbols follow Shell standard legend. [Note: Sample 618 should be shown as ranging throughout Beds 19 and 20.]

Paléontologie, Université de Brest, France; MRHN, Musée Royale d'Histoire Naturelle, Bruxelles, Belgium; SenckM, Senckenberg Museum, Frankfurt, West Germany; SedgM, Sedgwick Museum, Cambridge.

Suborder TORNOCERATINA Wedekind, 1917
Family TORNOCERATIDAE Arthaber, 1911
Genus CRASSOTORNOCERAS gen. nov.

Type species. Tornoceras ausavense crassum Matern, 1931.

Derivation of name. Alliterative couplet with specific appellation of type species. From Latin *crassus*, stout, referring to whorl form, and the genus *Tornoceras*.

Diagnosis. Small Tornoceratidae with subglobular inner whorls and small open umbilici with three to eight periodic constrictions per whorl following the biconvex course of the growth lines. Some specimens show weak ribs. Sutures simple tornoceratid usually with small lingulate lateral lobe.

Included species. C. crassum (Matern, 1931*a*, pl. 3, fig. 14*a*, *b*), *C. annissi* sp. nov. (herein), *C. belgicum* (Matern, 1931*b*, text-fig. 2), and *C. guestfalicum* (Frech, 1901, pl. 32*a*, fig. 8, refigured here as Pl. 16, figs. 14, 15).

Remarks. When Schindewolf (1936, p. 689) correctly recognized the oddity and extra umbilical lobe of *Goniatites ausavensis* Steininger (1853, p. 43, pl. 1, figs. 6, 6*a*, 7, 7*a*), and made it the type species of *Lobotornoceras*, this left unplaced the common and distinctive group for which the name *Crassotornoceras* is here applied.

There are several constricted forms referred to '*Aulatornoceras*' (but quite distinct from *A. auris*, the type species of that genus) which have similarities with some of the species referred here to *Crassotornoceras* but which differ in the possession of well-developed ventrolateral furrows. These include: '*A.*' *constrictum* (Steininger, 1853, p. 43, pl. 1, fig. 9, 9*a*) from the Büdesheimer Schiefer of the Eifel; '*A.*' *bickense* Wedekind (1917, p. 137), a *nomen nudem* possibly from the *holzapfeli* Zone at Bicken; and '*A.*' *loeschmanni* (Frech, 1902, pl. 5 (4), fig. 9*b*, *c*, refigured here as Pl. 16, figs. 16, 17) which shows a tabular venter but not the ventrolateral furrows which the first two share with the true *Aulatornoceras*. The time-span of this group is similar to that of *Crassotornoceras*. There is a range of possible interpretations of their relationships: either may be derived from the other; they may represent an evolving dimorphic pair; they may be quite independent. In the absence of any factual basis for knowing which of these possibilities is correct, it is hoped that the terminology used here will introduce more objectivity into the recording of these stratigraphically useful forms and posterity may solve the problem.

Horizons and range. Crassotornoceras has a restricted time range from the upper *cordatum* Zone probably only up to the *amblylobum* Zone (i.e. doIγ to doIIα). The genus is probably commonest in the *holzapfeli* Zone. The only certain record outside Europe occurs in the Angola Shale of upstate New York (Kirchgasser and House 1981, p. 49) just below records of *C. holzapfeli* in the Hanover Shale. There are only rare records in the *amblylobum* Zone, including two records by Frech (1902) from the Nehden Schiefer at Nehden and probably the record by Grüneberg (1925, p. 67, pl. 1, fig. 11, 11*a*, 11*b*) from the same level in the Herzkamp Syncline.

Crassotornoceras crassum (Matern, 1931)

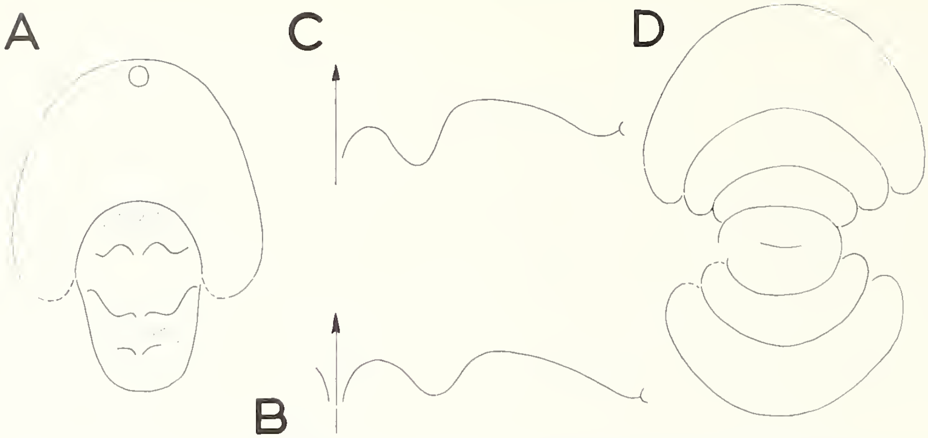
Plate 16, figs. 4, 8–11; text-figs. 3A, B, D, 4

1931 *Tornoceras ausavense crassum* Matern (1931*a*), p. 27, pl. 3, fig. 14*a*, *b*.

Holotype. SenckM XI 342*a* (*sic*, figured Matern 1931*a*, pl. 3, fig. 14*a*) from Büdesheim, Eifel, West Germany; Büdesheimer Schiefer, upper *cordatum* Zone, doIβ/γ.

Diagnosis. Species of *Crassotornoceras* with three to five constrictions which pass from the umbilicus to the venter; micromorphic.

Material. The holotype and about sixty other specimens collected by Matern, now in the Senckenberg Museum. Thirty-two specimens collected by M.R.H. from the type locality (BM(NH) C85201–85232). Belgian material is



TEXT-FIG. 3. A, B, D, *Crassotornoceras crassum* (Matern) showing whorl form, suture, and cross-section based on BM(NH) C85231 from the Büdesheimer Schiefer, Büdesheim, West Germany; A, B, ×6·9; D, ×15·3. C, *C. belgicum* (Matern), a suture based on the holotype, ×16·5.

from the Schistes de Matagne, some of it studied by Matern, and includes IG 83090 from Mariembourg and three specimens among IG 4630 from the quarry behind the church at Boussu en Fagne.

Dimensions	D	WW	WH	UW
Holotype SenckM XI 342*a*	7·2	3·3	—	—
Topotypes BM(NH) C85204	6·93	4·32	3·42	0·9
BM(NH) C85205	5·96	3·6	2·97	0·6
BM(NH) C85230	4·23	2·97	2·25	0·45
BM(NH) C85229	2·7	1·62	1·08	0·54

Description. The protoconch has not been dissected out but in BM(NH) C85231 its width is about 1·2 mm with a maximum diameter less than 0·93 mm. Early whorls show a rotund form, open umbilicus, maximum whorl width close to the umbilicus (text-fig. 3D), and depressed reniform whorl section. Whorl height increases

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EXPLANATION OF PLATE 16

Figs. 1–3. *Crassotornoceras belgicum* (Matern). MRHN unnumbered, holotype, from a quarry behind the church at Boussu en Fagne, Belgium, figured by Matern (1931*b*), ×8·7.

Figs. 4, 8–11. *C. crassum* (Matern). 4, MRHN unnumbered, from a quarry behind the church at Boussu en Fagne, Belgium, ×4. 8, 9, BM(NH) C85232, from the Büdesheimer Schiefer at Büdesheim, West Germany, ×5. 10, 11, BM(NH) C85201, from the Büdesheimer Schiefer at Büdesheim, West Germany, ×4.

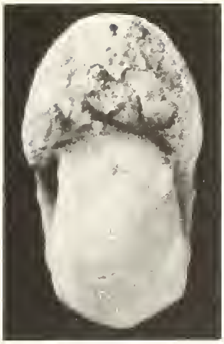
Figs. 5–7. *Aulatornoceras* cf. *A. auris* (Quenstedt). MRHN unnumbered, from a quarry behind the church at Boussu en Fagne, Belgium, ×3·5.

Figs. 12, 13. *C. annissi* sp. nov. SedgM H1541, holotype, from the Saltern Cove Goniatite Bed, Waterside Cove, Devon, ×5.

Figs. 14, 15. *C. guestfalicum* (Frech). BerlM c475/1, holotype, from the Nehden Schiefer at Nehden, West Germany, figured by Frech (1901, pl. 32*a*, fig. 8), ×3.

Figs. 16, 17. '*A.*' *loeschmanni* (Frech). BerlM c475/2, lectotype, from the Nehden Schiefer at Nehden, West Germany, figured by Frech (1902, pl. 5 (4), fig. 9*b*, *c*), ×3.

PLATE 16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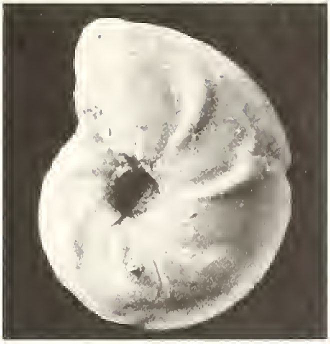
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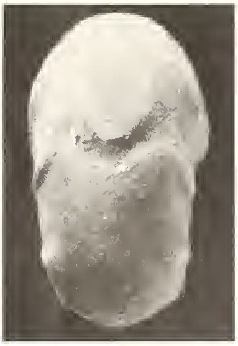
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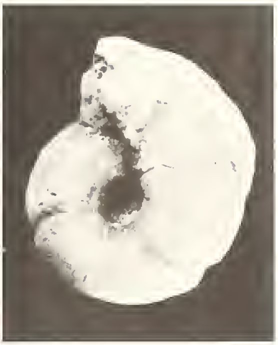
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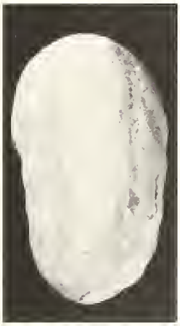
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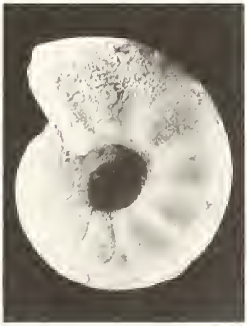
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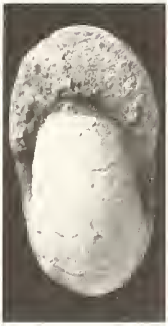
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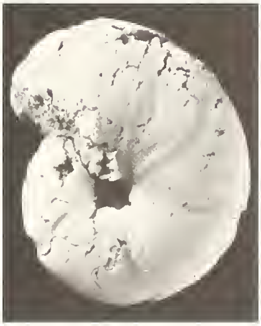
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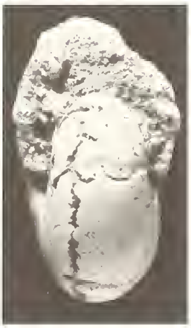
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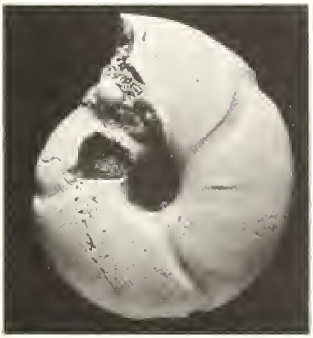
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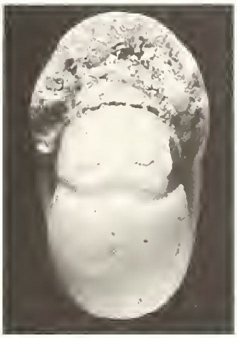
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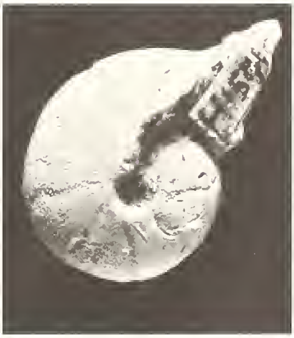
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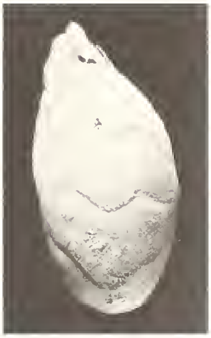
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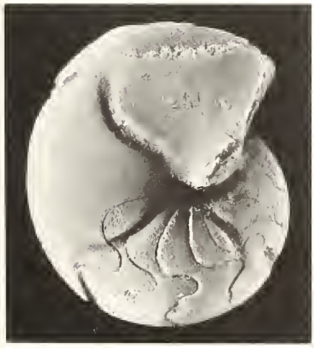
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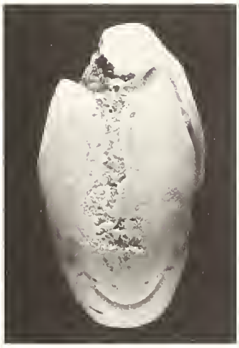
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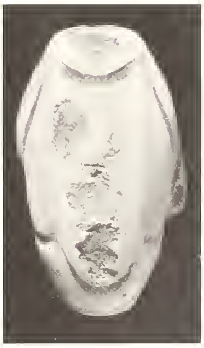
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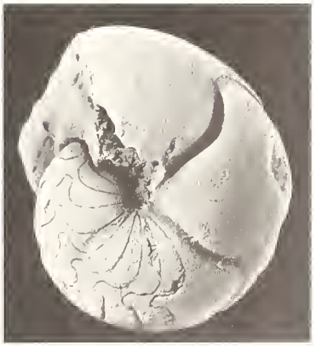
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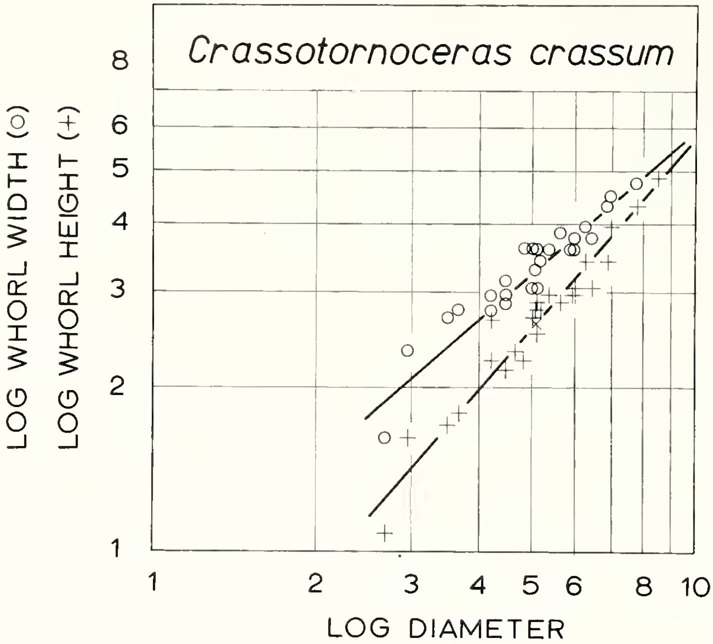
HOUSE and PRICE, *Crassotornoceras*, *Aulatornoceras*



TEXT-FIG. 4. Dimensions of *Crassotornoceras crassum* (Matern) based on twenty-four topotypes from the Büdesheimer Schiefer, Büdesheim, West Germany.

regularly in relation to width (text-fig. 3D); the statistics for the BM(NH) material are plotted in text-fig. 4. Growth lines are biconvex and the three to five constrictions per whorl follow the same course. None of the specimens exceeds 9 mm in diameter.

Remarks. This is a common form in the Büdesheim fauna, the rest of which is also micromorphic. There is no evidence of large specimens elsewhere but *Tornoceras* never shows inner whorls of this type.

Horizon and locality. The topotype material from Büdesheim was collected loose and this will certainly be true also for Matern's material. Details of this classic locality have been given by Clausen (1968*b*). In ammonoid terms the fauna is interpreted as of the upper *cordatum* Zone since *Crickites* has only been rarely recorded (Clausen 1968*b*) and is presumed to be from a rather higher level than the typical fauna. Clausen reported a determination by Ziegler of a sample from the type locality as having conodonts of the lower *gigas* Zone. Similarly the Belgian faunas, at least that from the Boussu en Fagne, are probably from levels below the entry of common *C. holzapfeli* rather higher in the Assise de Matagne. Mouravieff (1982) was unable to locate the typical deeper-water conodont guide fossils in this part of the Belgian sequence. In New York the level producing specimens of *Crassotornoceras* aff. *C. crassum* is from the Point Breeze Goniatite Bed in the early part of the Angola Shale, close to Lake Erie (Kirchgasser and House 1981): this part of the succession is referred to the *gigas* Zone by Oliver *et al.* (1969).

Crassotornoceras annissi sp. nov.

Plate 16, figs. 12, 13

1963 Gen. et sp. nov. House (1963*b*), p. 8.

Derivation of name. In honour of Dr. L. G. Anniss who made systematic goniatite collections from the type locality (Anniss 1927).

Holotype. SedgM H1541 from Saltern Cove Goniatite Bed, Waterside Cove, Paignton, Devon.

Diagnosis. Species of *Crassotornoceras* without ribs but with about eight constrictions concordant with biconvex growth lines and passing from the umbilical shoulder to the venter.

Dimensions	LD	WW	WH	UW
Holotype SedgM H1541	8·0	*c.* 5·1	4·5	0·8

Description. Shell form involute, subglobular but slightly compressed, with a small open umbilicus. Whorl section shows a well-rounded venter and convex lateral slopes reaching a maximum whorl width close to the umbilicus. The umbilical shoulder is sharply rounded and the wall vertical. Growth lines pass gently back from the umbilicus to form a very shallow lateral sinus and then a shallow ventrolateral salient; their course over the venter is not seen. Ornament consists of eight prominent shallow constrictions in the last whorl which apparently accord with the course of the growth lines. On the venter the constrictions are deeper than on the flanks and form a shallow broadly rounded sinus. The suture shows a V-shaped ventral lobe, a well-rounded ventrolateral saddle, a well-rounded lateral lobe, and a large broad latero-umbilical saddle with a steeper ventrad face. The two sutures seen are well spaced.

Remarks. This form has twice the average number of constrictions seen in *C. crassum*, none of the ninety topotypes of which has so many. Further, the constrictions pass slightly backward from the umbilical shoulder rather than forward as usual in *C. crassum*.

Horizon. As has been shown earlier (House 1963*b*), the goniatites from the Saltern Cove Goniatite Bed (from which all the indications are that this museum specimen comes) find their closest analogy with the *holzapfeli* Zone (doIδ), and this is taken to be the horizon. Nevertheless, van Straaten and Tucker (1972) have shown that the Saltern Cove Goniatite Bed is part of an intraformational slump, with other derived material set in an argillite matrix, which may be as young as the Platyclymenia Stufe.

Crassotornoceras belgicum (Matern, 1931)

Plate 16, figs. 1–3; text-fig. 3c

1931 *Tornoceras belgicum* Matern (1931*b*), p. 9, text-fig. 2.

Holotype. Specimen in MRHN figured by Matern (refigured here as Pl. 16, figs. 1–3), from the Schistes de Matagne (F3b) in a quarry behind the church at Boussu en Fagne, Belgium.

Diagnosis. Small species of *Crassotornoceras* with three constrictions in the last whorl; ribs developing on the outer flanks and numbering about six in the last whorl at D = 4·5 mm.

Description. The holotype is a small internal mould (D = 4·5 mm, WW = 2.7 mm) of compressed rotund form with a small open umbilicus and well-rounded whorl section. Growth lines, mainly inferred from ornament, pass almost prorsiradiately from the umbilicus with a shallow sinus and then project forward to a ventrolateral salient and rounded sinus on the venter. Three constrictions in the last whorl follow the course of the growth lines but are only well developed on the outer flanks and venter. About six ribs are formed in the last whorl, following approximately the course of the growth lines and constrictions, and developed in the outer part of the ventral sinus and dorsad part of the ventrolateral salient. Suture as illustrated in text-fig. 3c.

Remarks. From the same locality as the holotype is another specimen (Pl. 16, figs. 5–7) with similar ribbing but developed low on the flanks; additionally it shows the development of ventrolateral furrows. This specimen is referred to *Aulatornoceras* cf. *A. auris* (Quenstedt). Otherwise no material resembling this species has been described.

Horizon. We are indebted to Sarah Gatley (Trinity College, Dublin) for information that the locality indicates the upper part of the Schistes de Matagne (F3b), corresponding to the *holzapfeli* Zone.

Crassotornoceras guestfalicum (Frech, 1901)

Plate 16, figs. 14, 15

1901 *Tornoceras guestfalicum* Frech (1897–1902), pl. 32*a*, fig. 8.
1902 *Tornoceras loeschmanni* Frech (1902), pl. 5 (4), fig. 9*a* (only).

Holotype. BerlM c475/1, figured by Frech (1901, pl. 32*a*, fig. 8) from the Nehden Schiefer at Nehden (refigured here as Pl. 16, figs. 14, 15).

Remarks. When Frech first named this species he figured only the holotype, the character of which can be seen from the illustrations given here and his description. In 1902 he considered his name a homonym of *T. westfalicum* Holzapfel (1895, p. 104) and gave the name *T. loeschmanni* to two figured specimens, one of which was the holotype of *T. guestfalicum*; the other (illustrated here on Pl. 16, figs. 16, 17) is referred to '*A*.' *loeschmanni*. Although Frech clearly intended the name to be a replacement for *T. guestfalicum*, since the spelling is different from *T. westfalicum* it is not a homonym and his action under the *Rules* is not now valid. We do not consider the species congeneric. Thus we formally designate the second specimen of Frech (1902, pl. 5 (4), fig. 9*b*, *c*) as the lectotype of *loeschmanni* which we refer to the group similar to the true *Aulatornoceras* but without the ventrolateral furrows that characterize that genus.

Genus FALCITORNOCERAS gen. nov.

Type species. *Goniatites* (*Tornoceras*) *subundulatus* var. *falcata* Frech, 1887.

Derivation of name. Alliterative couplet with the specific name of type species. From Latin *falcatus*, scythe-shaped, referring to the form of the ribs, and the genus *Tornoceras*.

Diagnosis. Small Tornoceratidae with characteristic chevron ornament developed early in ontogeny, consisting of falcate ribs on the flank which continue over the venter. Ribs diminish in strength towards the smooth body chamber. Narrow umbilicus; tabulate venter developed in later whorls; narrow thin ventrolateral grooves may be present. Typical tornoceratid suture-line in early whorls, with asymmetric lateral lobe; umbilical lobe moves outside the seam in mature examples.

Included species and subspecies. *F. falcatum* (Frech, 1887, p. 465), *F. falciculum* sp. nov. (herein), *F. falciculum falciculum* subsp. nov. (herein), *F. falciculum constrictum* subsp. nov. (herein), *F. falciculum wagneri* subsp. nov. (herein).

Remarks. Apart from reference to the type species by Frech (1887, 1897–1902), none of these forms has been recognized in accounts of Famennian goniatites from western Europe (e.g. Wedekind 1917; Schindewolf 1923; Böhm 1935) probably because they have never been adequately described or illustrated. The origin of this group, whose members appear at or near the base of the *amblylobum* Zone (= the *curvispina* Zone of earlier authors), is unknown. Ancestors are *Tornoceras* or even '*Aulatornoceras*' but lack of these in the underlying *holzapfeli* Zone makes it difficult to determine from which *Falcitornoceras* was derived.

EXPLANATION OF PLATE 17

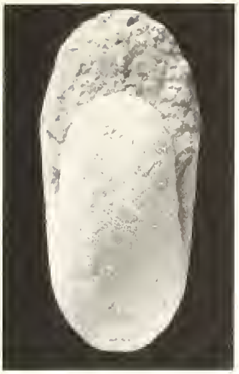
Figs. 1–7. *Aulatornoceras auris* (Quenstedt). Büdesheimer Schiefer at Büdesheim, West Germany. 1–4, SedgM H9942, neotype here designated, × 5. 5–7, SedgM H9943, topotype, × 3.

Figs. 8–10. *Polonoceras planum* Dybczyński. SedgM H9941, topotype, collected by Dr. H. Makowski from the lower Famennian at Sieclucki Brickpit, Kielce, Poland, × 2.

Figs. 11, 12. *Falcitornoceras falcatum* (Frech). BM(NH) C85169, collected by D. Korn from the Nehden Schiefer, Hohlweg, north-east of Nehden, West Germany (Mtb. 4517 Alme), × 3·5.

Figs. 13–16. *F. falciculum falciculum* subsp. nov. 13, 14, BM(NH) C85168, from the same locality and horizon as figs. 11, 12, × 3. 15, 16, LPB 4143, labelled 'base des Schistes de Porsguen, Ile Longue en Crozon, Finistère', France, × 4.

PLATE 17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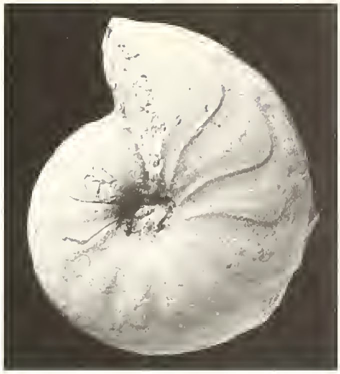
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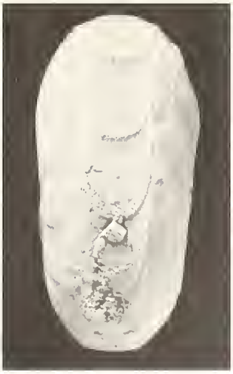
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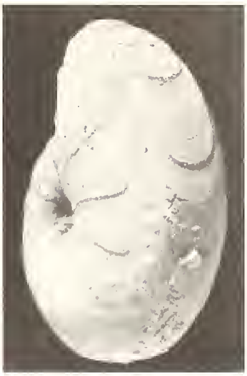
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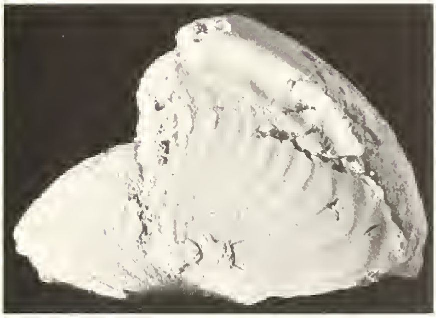
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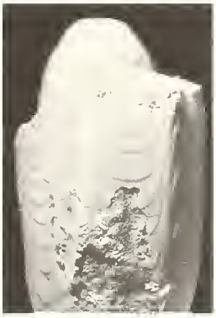
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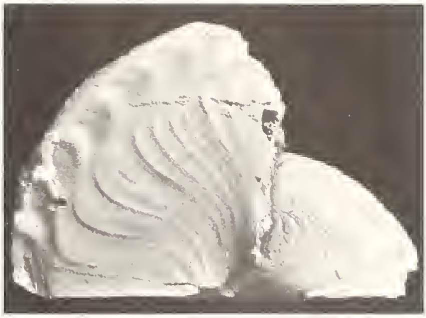
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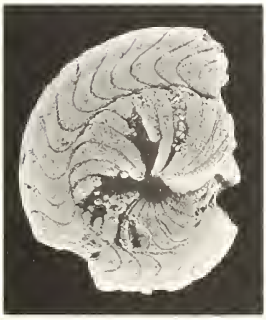
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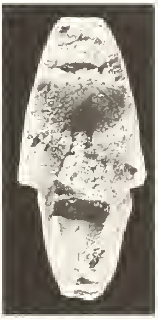
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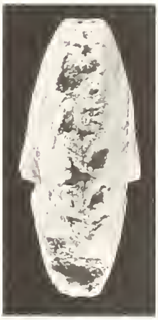
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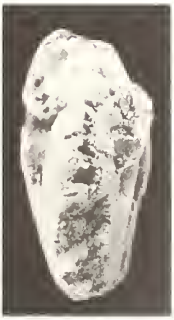
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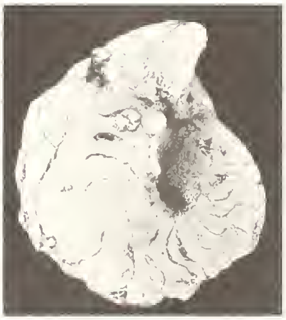
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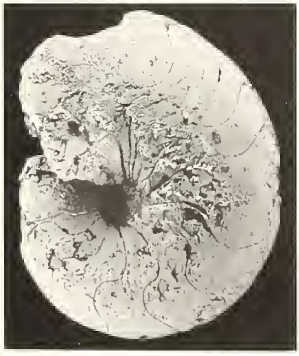
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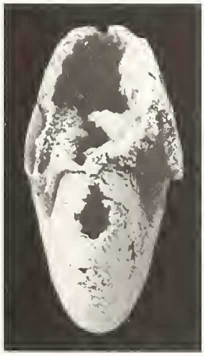
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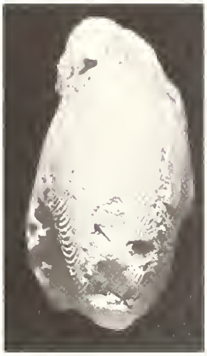
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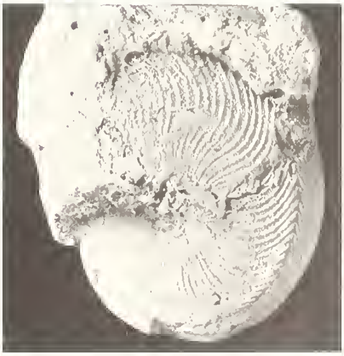
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HOUSE and PRICE, *Aulatornoceras*, *Polonoceras*, *Falcitornoceras*

Two other differently ribbed tornoceratids are known. '*A.*' *bicostatum* (Hall) occurs in the *amblylobum* Zone of New York State and has a late-stage ornament indistinguishable from some specimens of *F. falciculum* but, by contrast, its inner whorls are entirely smooth (House 1965). *T. amuletum* House from the Givetian of New York State develops coarse ribbing in early ontogeny, from nodes situated near to the umbilical shoulder. These gradually develop into widely spaced concave ribs running over the flank, with a V-shaped ventral sinus, but they become rursiradiate and falcate before disappearing at a diameter of 15 mm. The ribs, however, are quite different from those of *Falcitornoceras*.

Whorl width and whorl height are both plotted against diameter on logarithmic axes in text-fig. 5 but there seems to be little discrimination between the species and subspecies described here. Regression lines have been omitted from some of the plots because they overlap considerably and their inclusion would obscure many of the data points. The ratio of whorl width to whorl height plotted against diameter is useful in distinguishing between the taxa, as also is the plot of rib frequency against diameter (text-fig. 6). A reduced major axis has been computed using the method of Imbrie (1952).

Horizon and range. *Falcitornoceras* is known only from the Famennian *amblylobum* Zone and members have been reported from the Montagne Noire (Frech 1887, 1902), Thuringia (Zimmermann 1893), and Rostellec, Brittany (Frech 1897). Reports of lower Famennian ammonoids from Guadalmez by Groth (1914) and of *Reticuloceras superbilingue* from the same locality by Almela *et al*. (1961) may refer to occurrences of *Falcitornoceras*. Examples are described here from the lower Famennian shales at La Serre, the Nehden Schiefer at Nehden, and Guadalmez, central Spain. *F. falcatum* and *F. falciculum* have practically identical stratigraphic ranges, from Beds 17 to 26 in Trench C at La Serre (text-figs. 2, 9).

Specimens from the Montagne Noire. Most of the material used in this study was collected at La Serre, Cabrières, Hérault, either *in situ* in trenched sections or loose on the surface. The trenches (text-fig. 9) were dug under a research programme of Dr. R. Feist (University of Montpellier) and funded by the French CNRS. Trench C is situated 600 m east of the farmhouse La Roquette (68265e, 14006n) and exposes a sequence (text-fig. 2) of dolomitized Frasnian microsparites, uppermost Frasnian interbedded shales, cherts, and bituminous limestones (below Bed 13), lower Famennian shales and mudstones (Beds 14–22), middle and upper Famennian microsparites and nodular argillaceous limestones, and lower Tournaisian shales, mudstones, and oolites. Sample numbers (prefixed by LS), lithologies, and faunal ranges of the groups of interest here are shown on text-fig. 2. The highest manticoceratid collected *in situ* came from Bed 12; Bed 15 yielded only *Tornoceras* sp. and *Protornoceras* sp. The *Crickites* record shown came from levels corresponding to Beds 14 and 15, but in trench D according to information provided by Dr. Feist. *Falcitornoceras* was found as low as the base of Bed 17 in Trench C but the lowest *Cheiloceras*, currently used as the indicator for the base of the Nehden and Cheiloceras Stufe, occurred 5·5 m higher in Bed 20. Preliminary conodont dating provided by Dr. G. Klapper indicates that Bed 16 is already within the Famennian upper *triangularis* Zone.

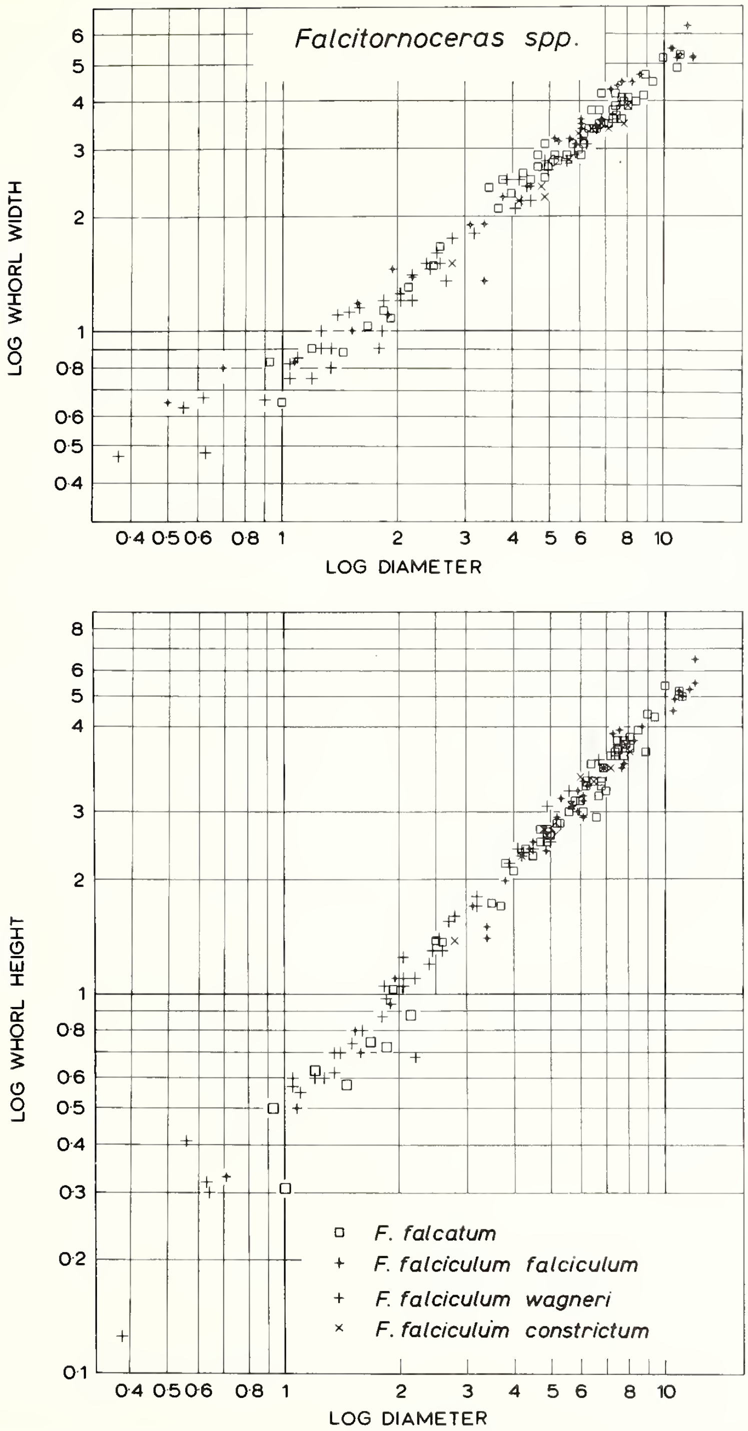
Falcitornoceras falcatum (Frech, 1887)

Plate 17, figs. 11, 12; Plate 18, figs. 5, 6; Plate 19, figs. 1–5, 9, 10, 13, 14; Plate 20, figs. 6, 7; text-figs. 7J–M

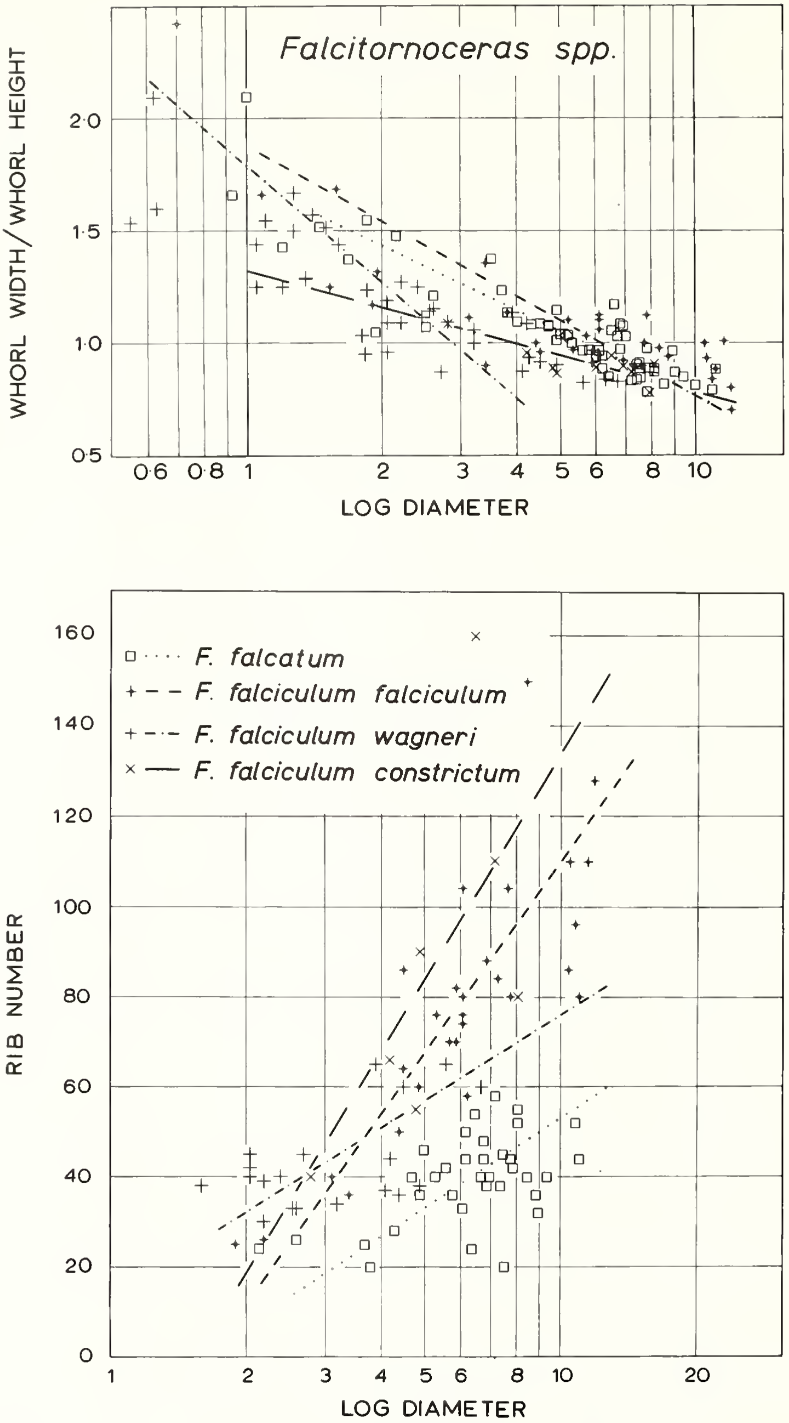
*1887 *Goniatites* (*Tornoceras*) *subundulatum* var. nov. *falcatum* Frech, p. 465.
1897 *Tornoceras falcatum* Frech; Frech (1897–1902), p. 177.
non 1897 *Tornoceras falcatum* Frech; Foord and Crick, p. 115, fig. 52.
1902 *Tornoceras subundulatum* var. *falcatum* Frech; Frech (1902), p. 50.

Neotype. BM(NH) C85039 (Pl. 19, figs. 1–3) from 600 m east of La Roquette, La Serre, Cabrières (68265e, 14006n), Hérault, France; Bed 17 (sample LS703), Trench C, *amblylobum* Zone, Famennian.

Material. Available for study besides the neotype were eleven paratypes (BM(NH) C85040–85050) and fifteen topotypes collected *in situ* (BM(NH) C85051–85065). A further eighteen specimens (BM(NH) C85068–85085), not included in the type series, were found loose at the surface within the area of the trenches (text-fig. 9); there is a single specimen from the nearby slopes of Val d'Izarne (BM(NH) C85067). BM(NH) C85169 was collected from the Hohlweg, north-east of the village of Nehden (West Germany, Mtb. 4517, Alme, r 34758, h 57000). All examples are preserved as haematitic internal moulds.



TEXT-FIG. 5. Dimensions of *Falcitornoceras* spp. based on 102 specimens. For further details see text. Regression lines omitted for clarity.



TEXT-FIG. 6. Graphs of the ratio whorl width/whorl height, and rib number, plotted against diameter for *Falcitornoceras* spp; reduced major axis regression lines are included.

Diagnosis. *Falcitornoceras* with prominent chevron-shaped ribs numbering twenty to sixty per whorl (mean 38, at mean diameter 6·4 mm; text-fig. 6), and diminishing in strength towards the body chamber. Ventrolateral grooves sometimes present but only on the body chamber.

Description. The neotype (Pl. 19, figs. 1–3), a relatively large specimen, attains a maximum diameter of 10 mm and shows well the ribbing (the characteristic feature of the species). The prorsiradiate ribs, about forty-two per whorl, are falcate with a very weak salient on the umbilical shoulder where the ribs commence. The ventrolateral shoulder is prominent and angular; the ventral sinus is deep and U-shaped. Over the flanks the rib cross-sectional profile approaches semicircular, with rib spacing being approximately half of rib width. Over the venter the ribs thicken, assuming a lunate shape with an asymmetrical cross-sectional profile, the orad face being the steeper. The body chamber extends for over 75% of a whorl, the first third of which has increasingly weaker and approximated ribs. The last rib occurs at a diameter of 6·5 mm; thereafter the body chamber is smooth but with a further third showing weak ventrolateral furrows occupying the same site as the ventrolateral salient of the ribbing.

Other specimens allow details of the ontogeny and specific variation to be determined. The protoconch and first half whorl are smooth (BM(NH) C85049). At early diameters, where the whorl section is depressed (D = 1 mm; WW/WH = 2·6 in BM(NH) C85049), ornament develops consisting of forwardly pointing chevron-shaped ribs on the outer flanks and a U-shaped ventral sinus. The whorl section, rounded and depressed on the inner whorls, becomes compressed at a diameter of 5·5 mm and above where the flanks are subparallel and the venter tabulate (text-fig. 7j).

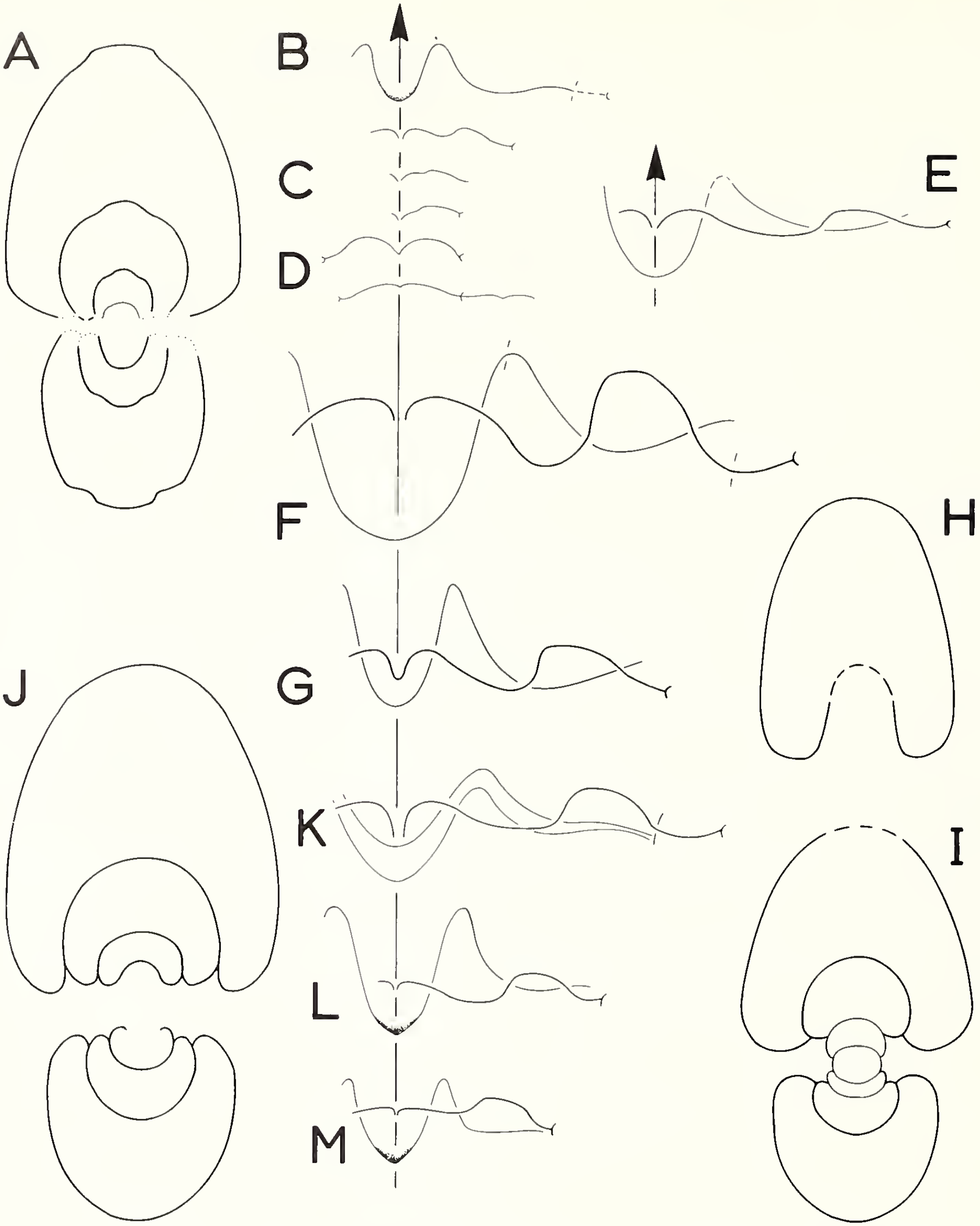
The ornament varies from specimen to specimen. Generally, the rib course becomes less angular and prorsiradiate in larger specimens (text-fig. 7k–m), and the ventral sinus more shallow. The gradual disappearance of the ribbing, to result in a smooth body chamber, is interpreted as a mature character and is associated with some septal approximation. The actual diameter where ribbing ceases was measured on twenty-one specimens (text-fig. 8); the mean diameter is 5·5 mm, in an apparently normal distribution, with a range from 2·7 mm (BM(NH) C85050) to > 9·4 mm (BM(NH) C85044; Pl. 19, figs. 13, 14) although these specimens were not from one population. In some smaller specimens (D = *c*. 2·5 mm) ribs are lost first from the flank, but persist on the venter which develops shallow ventrolateral grooves and a subcarinate shell form (BM(NH) C85048, C85050). Larger specimens lose their ribbing gradually, as on the neotype; when the ribs have disappeared there is one-third of a whorl with shallow ventrolateral grooves before these disappear too. One specimen (BM(NH) C85042; Pl. 19, figs. 4, 5) has three U-shaped constrictions on the venter of the body chamber. Large examples (e.g. BM(NH) C85043) have a funnel-shaped umbilicus. Growth curves for various parameters of species of *Falcitornoceras* are plotted in text-figs. 5, 6.

The partial sutural ontogeny is shown in text-figs. 7k–m. In large examples the umbilical lobe moves outside the seam. The course of the siphuncle can clearly be seen as it passes through the internal mould of the ribs. Usually septa are restricted to the ribbed part of the shell; no more than three are found beyond the point where the ornament is lost.

A single specimen (BM(NH) C85169; Pl. 17, figs. 11, 12), preserved as a haematitic internal mould and collected loose from the Nehden Schiefer at Nehden, is assigned to *F. falcatum*. This lacks ventrolateral grooves and shows a half-whorl of widely spaced falcate ribs.

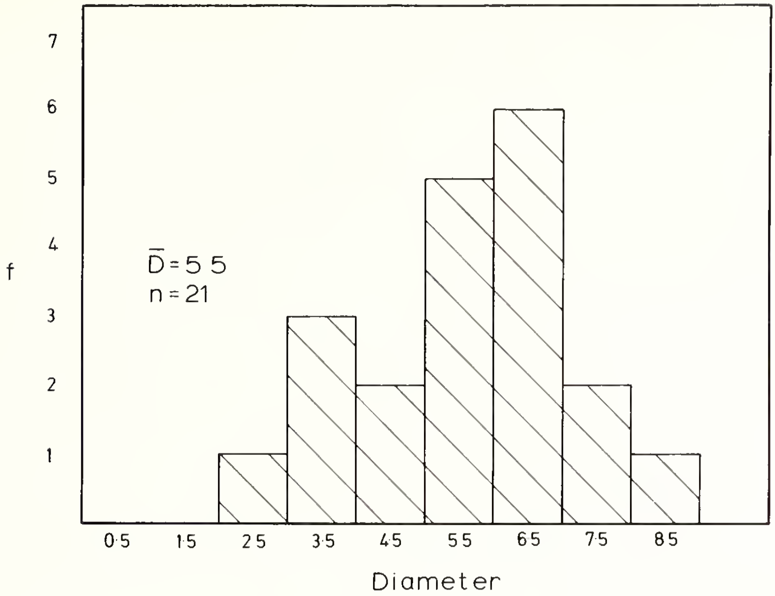
Dimensions	D	WW	WH	Ribs
Neotype BM(NH) C85039	7·3	3·9	4·4	44
BM(NH) C85044	9·4	4·5	5·3	40
BM(NH)C85042	7·55	3·68	4·35	20
	4·9	2·53	2·5	—
	3·5	2·38	1·73	—
	2·5	1·48	1·38	—
	1·85	1·13	0·73	—
	1·45	0·88	0·58	—

Remarks. No illustrations of the species *falcatum* Frech have ever been published, and the justification of it as this tornoceratid is based solely on Frech's initial description (1887, p. 465): 'Die var. [of *Gon*. (*Torn*.) *subundulatum* sp. nov.] *falcatum* zeichnet sich besonders im Ausseren durch das Vorhandsein sehr deutlicher, tief eingeschnittener Sichelrippen auf den Seiten aus, die jedoch auf der



TEXT-FIG. 7. Sutures, growth lines, and cross-sections of *Falcitornoceras* spp., all from BM(NH) specimens. A–D, *F. falciculum wagneri* subsp. nov. A, C85177, whorl cross-section, × 11; B, C85172, holotype, rib course at WW = 2·4 mm, × 10; C, C85178, early sutures (reversed for comparison) between D = 1·8 mm, WW = 1·25 mm and WW = 0·75 mm and WH = 0·5 mm, × 11; D, C85174, prosuture at D = 0·55 mm, WW = 0·63 mm, WH = 0·27 mm and first septum at WW = 0·8 mm, WH = 0·4 mm, × 15; specimens collected from Km 299·1 on the Madrid–Badajoz railway, 1 km south of Guadalmez, central Spain. E, *F. falciculum constrictum* subsp. nov. C85138, growth-line and a constriction (reversed) at D = 2·55 mm, WW = 1·5 mm, WH = 1·4 mm, × 20. F–I, *F. falciculum*

[*continued opposite*



TEXT-FIG. 8. Diameter at which the ribbed ornament is lost on *Falcitornoceras falcatum* from the lower Famennian at La Serre, south of Cabrières, Montagne Noire, France.

Wohnkammer meist vollig fehlen. Hier finden sich nun auf dem Rücken in regelmassigen Abstanden flache Einsenkungen. Ausserdem ist der Nabel sehr eng und die aussere Form mehr gerundet. Die Lobenlinie bleibt stets der das *Goniatites circumflexum* ähnlich. Beide Formen kommen in dem mittleren Oberdevon von La Serre nicht selten vor.' This description makes no mention of the ventrolateral grooves present on *F. falciculum*, the other ribbed species present at La Serre, and is clearly appropriate for the specimens described here. No evidence of the original material has been traced. A neotype is designated to clarify its diagnosis and to provide the first illustration of the species.

Zimmermann (1893) and Frech (1897) reported this species from Thuringia, associated with *Cheiloceras curvispina* which Frech (1897) used as the index fossil of the Cheiloceras Stufe. Frech's description seems to have been adequate for Foord and Crick (1897) to believe they had recognized the species amongst material in the British Museum (Natural History) from Hérault (BM(NH) C4791). The specimen they illustrated (fig. 52), however, has strong ventral constrictions, lacks coarse ribbing, and is referred to *F. f. constrictum*. The record of the species from Thuringia can be widened by reference to museum specimens in the Geologisch-Paläontologisches Institute, Marburg, collected by Denckmann and labelled 'Schmidts Grund bei Wallenfels', a locality in nearby Oberfranken.

F. falcatum has coarser less dense ribbing than other species of *Falcitornoceras*. At La Serre examples were found with rib frequencies of twenty-four to fifty-four per whorl at diameters of 5–10 mm. This compares with figures of sixty-four to one hundred and fifty for *F. f. falciculum*

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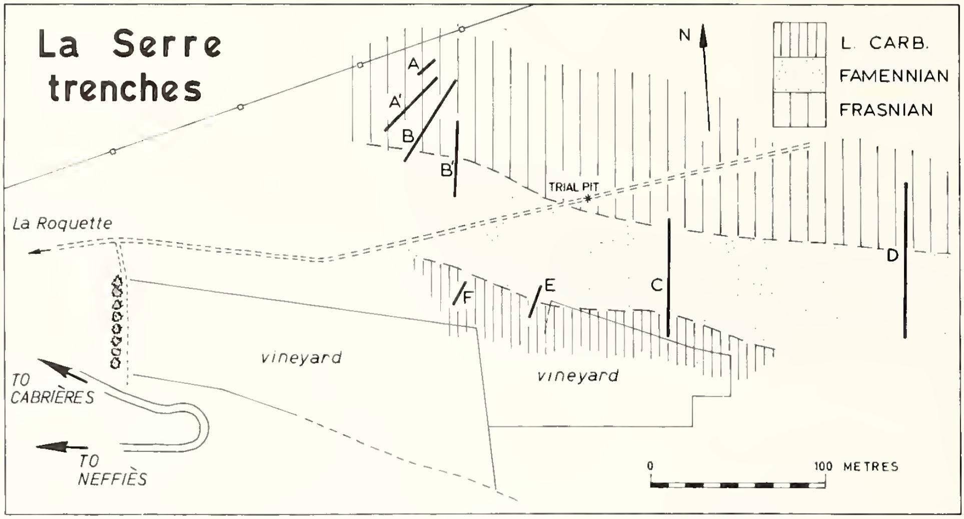
falciculum subsp. nov. F, C85090, growth-line and suture at D = 9·8 mm, WW = 5·8 mm, WH = 5·5 mm, × 10; G, C85086, holotype, growth-line and suture at WW = 2·7 mm, WH = 2·6 mm (reversed), × 11; H, C85093, whorl cross-section at WW = 5·3 mm, WH = 7·5 mm, × 5; I, C85092, whorl cross-section at D = 5·3 mm, WW = 3·2 mm, WH = 3·3 mm, × 10. J–M, *F. falcatum* (Frech). J, C85042, whorl cross-section at D = 7·5 mm, WW = 3·7 mm, WH = 4·4 mm, × 10; K, C85044, suture and rib at WW = 3·9 mm, WH = 4·2 mm, × 9; L, C85043, suture and growth-line at WW = 2·0 mm, WH = 1·8 mm, × 10; M, C85046, suture and growth-line at WW = 2·0 mm, WH = 2·6 mm, × 10.

with which it occurs. That this distinction in rib density is not determined by an arbitrary limit is clear from text-fig. 6 on which the species plot in distinct and divergent fields. *F. falcatum* also lacks the ventrolateral grooves which appear at the nepionic constriction in *F. falciculum* (Pl. 20, figs. 3–5).



TEXT-FIG. 9. Map showing the position of trenches dug at La Serre, south of Cabrières, Hérault, Montagne Noire, France, excavated during the research programme of Dr. R. Feist (University of Montpelier) and based on a survey by J.D.P. The section shown in text-fig. 2 is at Trench C.

Horizon and range. At La Serre *F. falcatum* was collected between Beds 17 (sample LS 703; refer to text-fig. 2 for location of sample numbers) and 26 (sample LS 808), and it appears in the record some 5·5 m below the first *Cheiloceras* in Bed 20 (sample LS 796).

Falcitornoceras falciculum sp. nov.

Derivation of name. From Latin *falcicula*, diminutive of Latin *falx*, sickle, alluding to the thin sickle-shaped ribs present on this species.

Holotype. See nominate subspecies.

EXPLANATION OF PLATE 18

Figs. 1–17. *Falcitornoceras* gen. nov. All except 15–17 preserved as haematitic moulds. 1–10, 13, 14, from lower Famennian shales, around 600 m east of La Roquette, La Serre, Cabrières, Hérault, France.

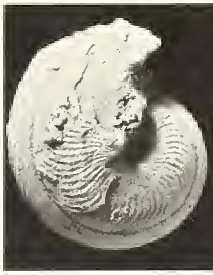
Figs. 1, 2, 9–14, 17. *F. falciculum falciculum* subsp. nov. 1, 2, BM(NH) C85091, ×5. 9, 10, BM(NH) C85089, from Trench C (sample LS 808), ×8. 11, 12, BM(NH) C85066, mature individual which has lost its ribs on the body chamber, Val d'Isarne (628), Cabrières, Hérault, France, ×8. 13, 14, BM(NH) C85086, holotype, from Trench C (sample LS 738), ×5. 17, LPB 5542*b*, external mould labelled 'Formation des Marettes La Rabine en La Chapelle Chaussée, Ille et Vilaine', France, ×4.

Figs. 3, 4, 7, 8. *F. falciculum constrictum* subsp. nov. 3, 4, BM(NH) C85138, showing U-shaped constrictions over the venter, from Trench C (sample LS 818), ×8. 7, 8, BM(NH) C85139, ×6.

Figs. 5, 6, *F. falcatum* (Frech). BM(NH) C85041, from Trench C (sample LS 818), ×8.

Figs. 15, 16. *F. falciculum* sp. nov. Nodule band in the Nehden Schiefer, Nehden, West Germany (Mtb. 4517 Alme). 15, BM(NH) C85171, ×8. 16, BM(NH) C85170, ×8.

PLATE 18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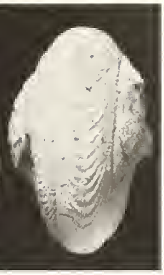
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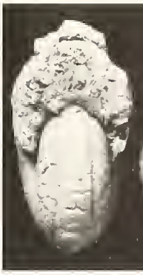
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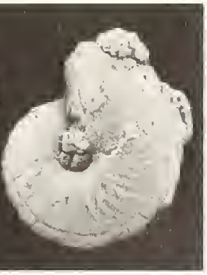
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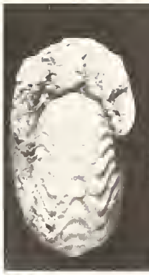
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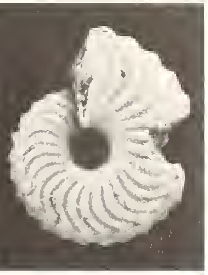
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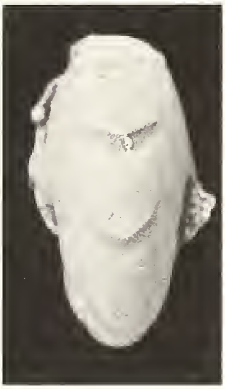
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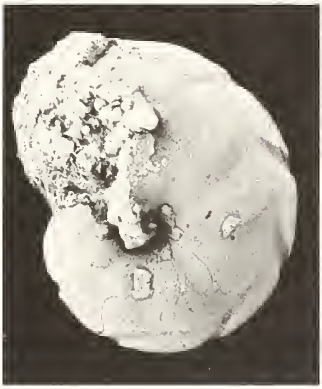
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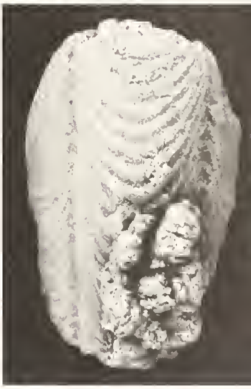
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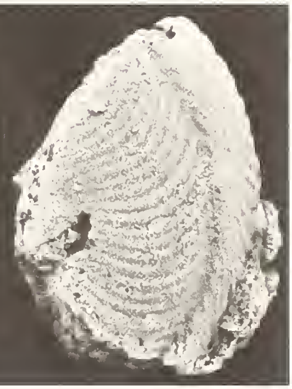
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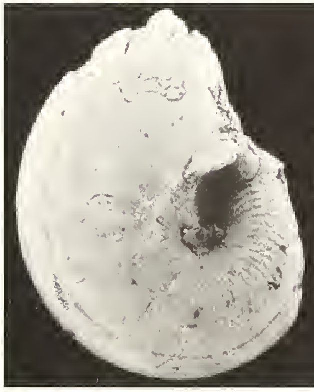
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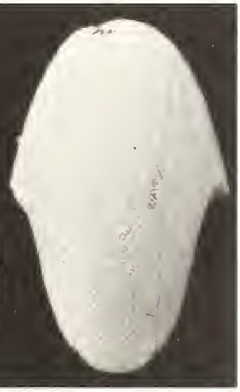
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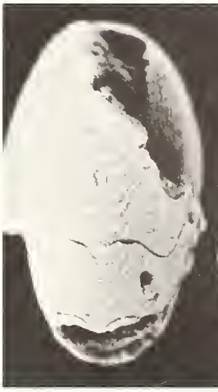
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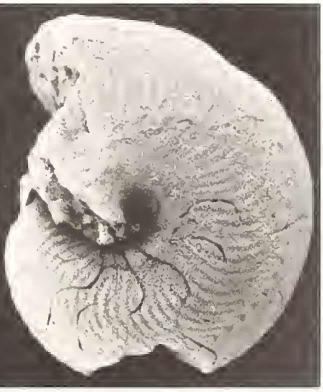
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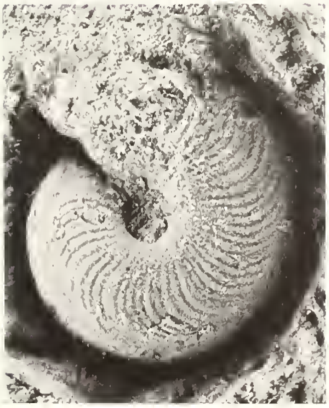
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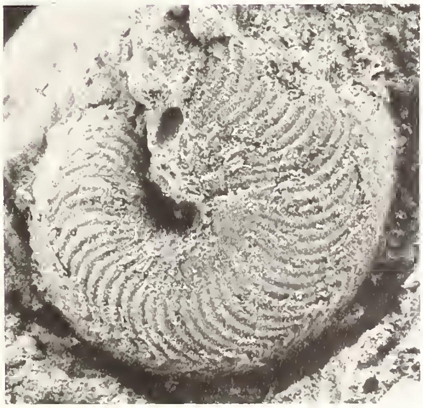
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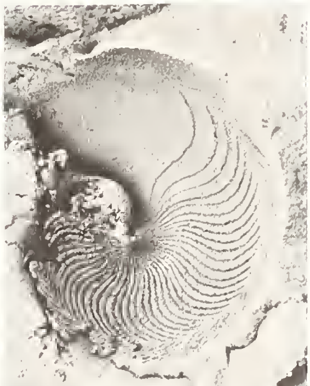
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HOUSE and PRICE, *Falcitornoceras*

Diagnosis. Falcitornoceras with chevron-shaped ribs numbering twenty-five to one hundred and fifty per whorl and diminishing in strength towards the body chamber. Ventrolateral grooves may be present at the nepionic constriction but may be lost in mature specimens.

Remarks. Three subspecies, *constrictum*, *falciculum*, and *wagneri*, are erected here, the last two distinguished solely by their ribbing frequencies, and the first by its numerous lateral constrictions. Two specimens of *F. falciculum* (BM(NH) C85170, C85171; Pl. 18, figs. 15, 16) from a calcareous nodule in the Nehden Schiefer at Nehden, cannot easily be assigned to any of these subspecies. They are preserved complete with shell and have a ribbing frequency (sixty ribs per whorl) intermediate between *falciculum* and *wagneri*. The ribs have a rounded cross-sectional shape and the ventrolateral grooves are only weakly developed. No constrictions are visible, although generally these can be seen only on internal moulds.

Horizon and range. As for the genus. Conodonts extracted from the matrix of the specimens from Nehden were kindly identified by Professor W. Ziegler (Senckenberg Museum, Frankfurt) and indicate the upper *crepida* to lower *rhomboidea* Zones, Famennian.

Falcitornoceras falciculum falciculum subsp. nov.

Plate 17, figs. 13–16; Plate 18, figs. 1, 2, 9–14, 17; Plate 19, figs. 16, 17;
Plate 20, figs. 8–10, 12, 13; text-figs. 7F–I.

1935 *Tornoceras sandbergeri* Foord and Crick; Böhm, p. 55, fig. 9.

Holotype. BM(NH) C85086 (Pl. 18, figs. 13, 14; text-fig. 7G) from La Serre; sample LS 738, Bed 21, Trench C, *amblylobum* Zone, Famennian.

Material. Nine specimens (BM(NH) C85088–85096) collected from the type locality are selected as paratypes, together with one (BM(NH) C85087) from the nearby slopes of Val d'Isarne. Eleven specimens are designated topotypes (BM(NH) C85097–85107). A further twenty-five specimens (BM(NH) C85108–85132), not included in the type series, were collected from scree at La Serre; one (BM(NH) C85135) at Col du Puech de la Suque, St. Nazaire de Ladarez, Hérault; one (BM(NH) C85134) from La Tourrière, Cabrières, Hérault; and two (BM(NH) C85167, C85168) from the Nehden Schiefer at Nehden. Six specimens from Brittany (LPB 5542, 5543*a*, *b*, 5544*a*–*c*) were labelled 'Formation des Marettes, La Rabine en La Chapelle Chausée' (Ille et Vilaine, see Babin and Paris 1973); and two (LPB 4136, 4143) were labelled 'base du Schistes du Porsguen, Ile Longue en Crozon', Finistère.

Diagnosis. F. falciculum with fine concave or falcate ribs, twenty-five to one hundred and fifty per whorl (mean 78 at mean diameter 6 mm; text-fig. 6). Compressed whorl form with tabulate or arched venter bounded by two thin ventrolateral grooves developed early in ontogeny.

EXPLANATION OF PLATE 19

Figs. 1–17. *Falcitornoceras* gen. nov. All except 6–8 and 16, 17 preserved as haematitic internal moulds and are from lower Famennian shales, around 600 m east of La Roquette, La Serre, Cabrières, Hérault, France.

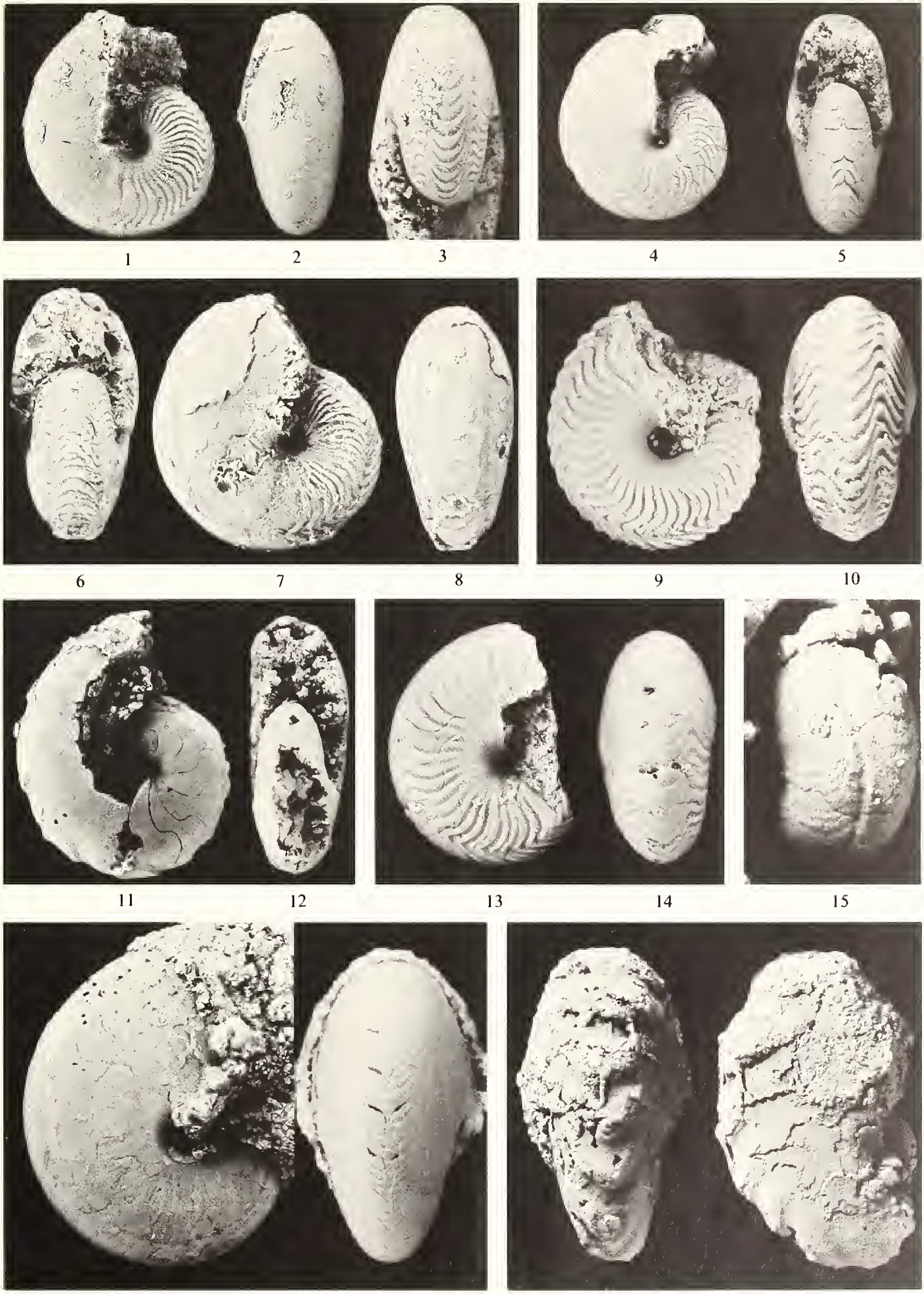
Figs. 1–5, 9, 10, 13, 14. *F. falcatum* (Frech). 1–3, BM(NH) C85039, neotype, side view and two ventral views half a whorl apart, from Trench C (sample LS 703), ×4 (1, 2) and ×5 (3). 4, 5, BM(NH) C85042, with ventral constrictions on the body chamber, ×4·5. 9, 10, BM(NH) C85045, ×6. 13, 14, BM(NH) C85044, ×4.

Figs. 6–8. *F. falciculum wagneri* subsp. nov. BM(NH) C85172, holotype from Km 299·1 on the Madrid–Badajoz railway, 1 km south of Guadalmez, central Spain, ×6.

Figs. 11, 12, 15, 18, 19. *F. falciculum constrictum* subsp. nov. 11, 12, BM(NH) C85136, holotype from Trench C (sample LS 783), ×4. 15, 18, 19, BM(NH) C85137, ribbed inner whorls and views of smooth, constricted venter and flanks of body chamber, from Trench C (sample LS 703), ×10 (15) and ×4 (18, 19).

Figs. 16, 17. *F. falciculum falciculum* subsp. nov. BM(NH) C85167, from the Nehden Schiefer at the Hohlweg, north-east of Nehden, West Germany (Mtb. 4517 Alme), ×5.

PLATE 19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HOUSE and PRICE, *Falcitornoceras*

Dimensions	D	WW	WH	Ribs
Holotype BM(NH) C85086	6·9	3·6	3·9	88
	5·2	3·2	2·9	—
Paratypes BM(NH) C85092	5·33	3·15	3·25	76
	3·8	2·25	1·98	—
	1·95	1·45	1·10	—
	1·58	1·18	0·7	—
	1·08	0·83	0·7	—
	0·7	0·8	0·33	—
	0·5	0·65	—	—
BM(NH) C85093	12·0	5·25	7·5	128

Description. The holotype (Pl. 18, figs. 13, 14; text-fig. 7G), although the best preserved of the specimens found *in situ*, illustrates the features of the subspecies rather poorly. It has eighty-eight falcate ribs in the whorl prior to a diameter of 6·9 mm. The flatly rounded venter is bounded by two shallow grooves. The suture is shown in text-fig. 7G.

Other specimens allow the subspecies to be described in more detail. The protoconch has not been observed. Early whorls up to 2 mm diameter have strong concave ribs over the flank, twenty-six per whorl, and a tabular venter bounded by clearly visible grooves (BM(NH) C85094, at D = 2·2 mm; Pl. 20, figs. 8–10). Later the ribs become more densely spaced, thirty-six per whorl at D = 3·4 mm (BM(NH) C85088, Pl. 20, figs. 12, 13).

The whorl section (text-fig. 7H, I), with globose inner whorls, develops rounded flanks but becomes compressed by a diameter of 6·5 mm (text-fig. 7I). Ventrolateral grooves are still present on the largest specimen (BM(NH) C85093) at a whorl height of 7·5 mm. The dense ribbing persists throughout the phragmocone and on to the body chamber; BM(NH) C85096 has a body chamber one whorl in length, all of which is ribbed; BM(NH) C85090, 11·6 mm in diameter and wholly septate, has ribs which diminish in strength during the last quarter whorl. But BM(NH) C85095 loses its ribs by a diameter of 5·8 mm, having a body chamber three-quarters of a whorl in length, the first third of which is densely ribbed and smooth thereafter but with ventrolateral grooves and weak plications. The same modification in ornament is seen on BM(NH) C85066 (Pl. 18, figs. 11, 12) which loses all its ribs by a diameter of 4 mm. At the mean diameter for this sample (5·9 mm), the mean number of ribs per whorl is 80. The sutural ontogeny is similar to *F. falcatum*, but on BM(NH) C85090 (D = 11·6 mm) (text-fig. 7F) the umbilical lobe lies outside the seam and the lateral saddle is high, rounded, and asymmetric.

Two relatively large (D = 11 mm) specimens, preserved as haematitic internal moulds and collected from the Nehden Schiefer at Nehden (Mtb. 4517 Alme), show only the first few degrees of body chamber (BM(NH) C85167, Pl. 19, figs. 16. 17; BM(NH) C85168, Pl. 17, figs. 13, 14). On BM(NH) C85167 ribs are present throughout the whole of the last whorl seen but become coarser and more widely spaced towards the body chamber. Ribs are still visible over the venter at a stage when they are much reduced in strength over the flanks. Coincident with the decrease in rib strength and frequency is the disappearance of marked ventrolateral grooves. BM(NH) C85168 has fine ribbing but lacks ventrolateral grooves.

Horizon and range. At La Serre this subspecies occurs between Beds 17 (sample LS 703) and 26 (sample LS 808) in Trench C, in and below the *amblylobum* Zone, Famennian.

Falcitornoceras falciculum constrictum subsp. nov.

Plate 18, figs. 3, 4, 7, 8; Plate 19, figs. 11, 12, 15, 18, 19; text-fig. 7E

1897 *Tornoceras falcatum* Frech; Foord and Crick, p. 115, fig. 52.

Derivation of name. From Latin *constrictum*, narrow, referring to the constrictions of the ventral area.

Holotype. BM(NH) C85136 (Pl. 19, figs. 11, 12) from La Serre (see under *F. falcatum*); sample LS 783, Bed 22, Trench C, *amblylobum* Zone, Famennian.

Material. Five specimens (BM(NH) C85137–85141) are designated as paratypes, and a further seventeen (BM(NH) C85142–85158) as topotypes.

Diagnosis. Like *F. f. falciculum* but with a different late-stage shell form consisting of narrower whorl width and a venter with V-shaped constrictions numbering at least six per whorl, and in some examples extending across the flank to form weak plications.

Dimensions	D	WW	WH	Ribs
Holotype BM(NH) C85136	6·0	3·3	3·7	—
Paratypes BM(NH) C85138	2·8	1·5	1·38	40
BM(NH) C85139	6·9	3·5	3·9	—

Description. The holotype is a relatively large specimen (D = 10 mm) and shows rather well the late stage ornament which distinguishes this subspecies. The earliest part of the last whorl has finely ribbed flanks bounded by thin ventrolateral grooves. Only one ventral constriction is visible, on the ribbed portion; otherwise the venter is damaged. The ribbing strength diminishes over the last half whorl so that by the position of the last septum (at D = 6 mm) there are no ribs and the ventrolateral grooves are much reduced in depth. The last half whorl is body chamber, with six ventral constrictions which run into the ventrolateral groove.

Other specimens allow details of the ontogeny and variation to be determined. Early whorls were not seen. The shell form is like *F. f. falciculum*, except in large specimens where the whorl width is less, but no specimens were well enough preserved to be sectioned. The smallest specimen seen (BM(NH) C85138; Pl. 18, figs. 3, 4) has forty concave ribs, ventrolateral grooves, and six weak ventral constrictions. The last three septa are approximated (at D = 2·5 mm) suggesting that, although small, this specimen may be mature. The body chamber is preserved through 90°. Two slightly larger specimens, BM(NH) C85141 (D = 4·2 mm) and C85139 (Pl. 18, figs. 7, 8), have a similar ornament but the constrictions are deeper, more extensive, and associated with shallow plications on the flanks near to the umbilicus. This modification of the ornament is even more pronounced on BM(NH) C85140 (D = 4·8 mm). The holotype has a smooth body chamber; the smallest specimen on which a smooth body chamber is developed is BM(NH) C85139, where the ribbing disappears at a diameter of 5 mm, leaving smooth plicate flanks with strong ventral constriction. At similar diameters on BM(NH) C85142 there is no plication, only ventral constrictions and ventrolateral grooves. The largest specimen seen, BM(NH) C85137 (D < 13 mm; Pl. 19, figs. 15, 18, 19), has closely spaced constrictions numbering five in one-quarter whorl, and smooth compressed flanks which run into the high arched venter. The suture line (text-fig. 7E) does not differ from *F. f. falciculum*.

Remarks. These specimens differ only slightly from *F. f. falciculum* which was collected from the same stratigraphic levels. Examples less than 5 mm in diameter are difficult to distinguish but, when larger than this, that subspecies has a shell and more especially a body chamber which retains fine ribbing and ventrolateral grooves (although it may become smooth), whereas *F. f. constrictum* develops constrictions and a smooth plicate body chamber. No specimens were found with only few constrictions which might be considered as being intermediate between these two subspecies. This suggests that they are distinct and separate, although they could represent sexual dimorphs. Hitherto sexual dimorphism in the Tornoceratidae has been postulated only on the basis of bimodal size distribution (Makowski 1962).

Horizon and range. This subspecies is only known from the Famennian *amblylobum* Zone at La Serre, Hérault, in Trench C between Beds 17 (sample LS 703) and 26 (sample LS 818).

Falcitornoceras falciculum wagneri subsp. nov.

Plate 19, figs. 6–8; Plate 20, figs. 1–5, 11, 14–18; text-fig. 7A–D

?1961 *Reticuloceras superbilingue* Bisat; Almela *et al.*, p. 211, fot. 7, 8, 11, 12.

Derivation of name. Named for Drs. R. H. Wagner and C. H. Th. Wagner Gentis who collected the material described here.

Holotype. BM(NH) C85172 (Pl. 19, figs. 6–8; text-fig. 7B) from Km 299·1 on the Madrid–Badajoz railway, 1 km south of Guadalmez, central Spain (see Almela *et al.* 1961); Lower Famennian Shales.

Material. The holotype, six paratypes (BM(NH) C85173–85178), and twenty-two topotypes (BM(NH) C85179–85200) preserved complete or as internal moulds in yellow weathering calcareous mudstone.

Diagnosis. F. falciculum with twenty-five to sixty-five (mean 43, at diameter 3·1 mm) falcate ribs per whorl, with prominent ventrolateral grooves developed at the nepionic constriction and persisting until the mid-stage of the otherwise unornamented body chamber.

Dimensions	D	WW	WH	Ribs
Holotype BM(NH) C85172	6·7	3·5	4·1	60
	5·0	2·65	2·5	—
Paratypes BM(NH) C85175	2·55	1·6	1·4	33
	2·45	1·45	1·3	—
	1·83	1·0	1·05	—
BM(NH) C85174	0·55	0·63	0·41	—
	1·05	0·75	0·6	—
Topotype BM(NH) C85195	0·37	0·47	0·13	—

Description. The holotype (BM(NH) C85172, Pl. 19, figs. 6–8) shows only the features of the mature shell; the ontogeny is described from other specimens. The spindle-shaped protoconch (BM(NH) C85195) quickly increases in whorl height resulting in a globose shell form at early diameters (BM(NH) C85174, Pl. 20, figs. 1, 2, 11). The nepionic constriction was observed on six specimens (BM(NH) C85176, Pl. 20, figs. 3–5; C85186, C85193, C85194, C85196, C85197), at diameters 0·9–1·05 mm. The constriction is visible more clearly on the internal mould and is prorsiradiate and concave over the flank, with a shallow ventral sinus. The ornament consists of concave ribs with a U-shaped ventral sinus and clear ventrolateral grooves, and appears at the nepionic constriction as demonstrated for *Tornoceras* by House (1965). The shell form (text-fig. 7A) is globose in early whorls, with a maximum whorl width midway across the flanks, a tabulate venter, and ventrolateral grooves; compressed flanks develop at a diameter of 3 mm and the point of maximum whorl width migrates to the umbilical shoulder. A funnel-shaped umbilicus is formed. Growth curves for various parameters are shown in text-figs. 5, 6.

The ribbing maintains its concave prorsiradiate course over the flanks (Pl. 20, fig. 4) up to the point where an umbilical shoulder is formed (D = *c*. 3 mm); here a weak umbilical salient is developed (text-fig. 7B), giving the ribs a true falcate shape. The ribs have an angular asymmetrical profile when viewed in cross-section, with the steeper face orad, rather like those on *F. falcatum*. The last three ribs on some specimens (e.g. BM(NH) C85172, Pl. 19, figs. 6–8) are widely spaced and subdued, after which the body chamber is smooth with only weak ventrolateral grooves persisting for about a third of a whorl before they too disappear. The smooth body

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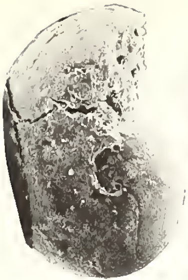
EXPLANATION OF PLATE 20

Figs. 1–5, 11, 14–18. *Falcitornoceras falciculum wagneri* subsp. nov. 1, 2, BM(NH) C85174, internal mould of protoconch, × 30. 3–5, BM(NH) C85176, showing the nepionic constriction and appearance of the ventrolateral furrows and ribs at that point, × 25. 11, BM(NH) C85174, prosuture and first suture, × 55. 14, BM(NH) C85173, × 10. 15–17, BM(NH) C85175, × 15. 18, BM(NH) C85173, × 20. All specimens collected by Dr. R. H. Wagner and C. H. Th. Wagner-Gentis from Km 299·1 on the Madrid–Badajoz railway, 1 km south of Guadalmez, central Spain.

Figs. 6, 7. *F. falcatum* (Frech). BM(NH) C85040, haematitic internal mould collected from lower Famennian shales, about 600 m east of La Roquette, La Serre, Cabrières, Hérault, France, × 15.

Figs. 8–10, 12, 13. *F. falciculum falciculum* subsp. nov. lower Famennian shales, about 600 m east of La Roquette, La Serre, Cabrières, Hérault, France. 8–10, BM(NH) C85094, × 18. 12, 13, BM(NH) C85088, from Trench C (sample LS 703), × 10.

All scanning electron micrographs.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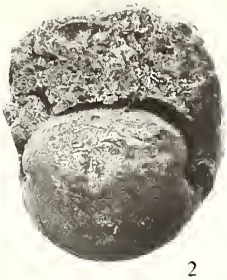
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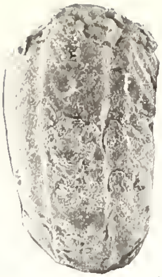
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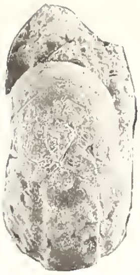
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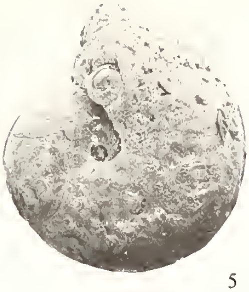
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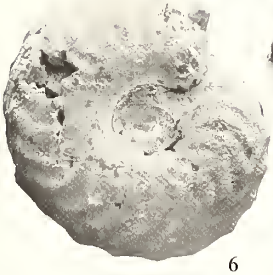
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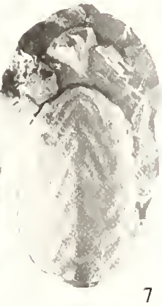
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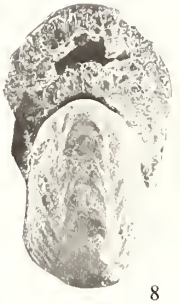
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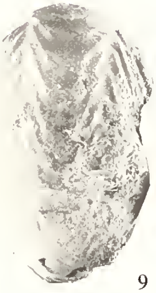
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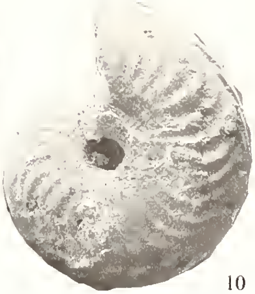
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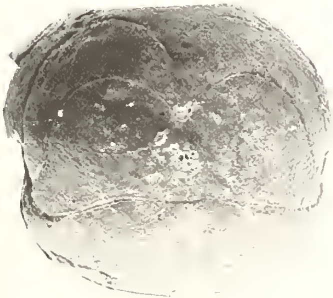
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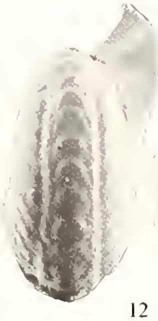
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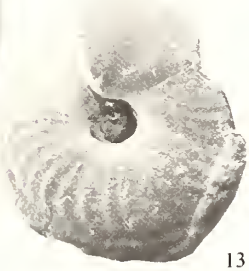
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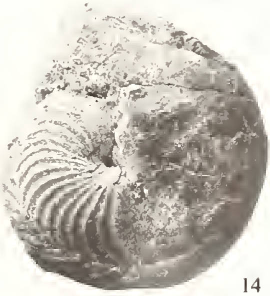
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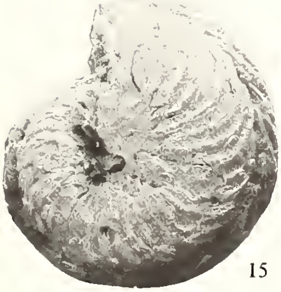
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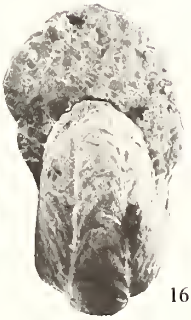
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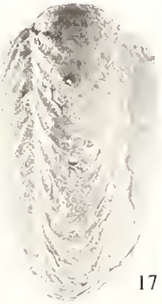
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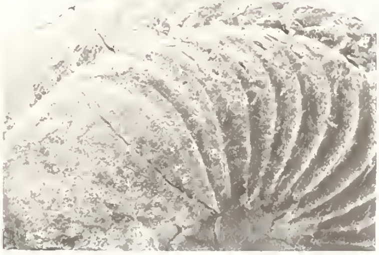

HOUSE and PRICE, *Falcitornoceras*

chamber extends for half a whorl. One specimen (BM(NH) C85183) has no ventrolateral grooves at a diameter of 1·8 mm, much denser (sixty-five per whorl) and finer ribs, and a more globose shell form.

The suture is known only from juvenile examples (text-fig. 7C, D); the prosuture and first suture are visible in Pl. 20, fig. 11.

Remarks. The material from which these specimens were extracted contained many juvenile goniatites, most of which were just early whorls and so could not be identified. *F. f. wagneri* is distinguished from *F. f. falciculum* by its lower rib density (mean 43 per whorl, compared with 80). *F. falcatum* has a similar number of ribs (mean 39 per whorl) but lacks the ventrolateral grooves formed at the nepionic constriction.

Horizon and range. Other species of *Tornoceras* and *Lobotornoceras* were found together with *F. f. wagneri* but there were no *Cheiloceras*, suggesting that this occurrence was low in the *amblylobum* Zone, Famennian. Preparation of conodont samples produced no stratigraphically useful forms.

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THE MORPHOLOGY AND ECOLOGY OF A MOUND-BUILDING CORALLINE ALGA (*NEOGONIOLITHON STRICTUM*) FROM THE FLORIDA KEYS

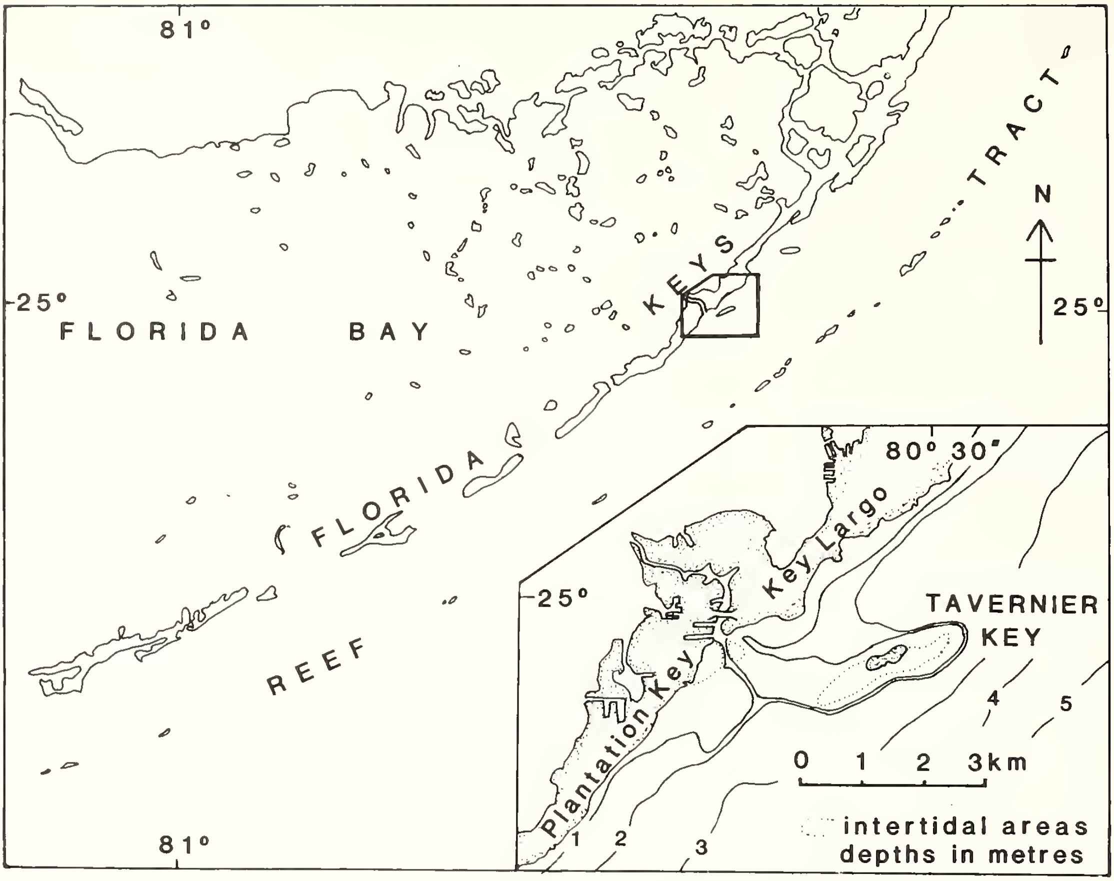
by DANIEL W. J. BOSENCE

ABSTRACT. The coralline alga *Neogoniolithon strictum* Setchell and Mason, 1943 is a major component of carbonate mound-building communities in the Florida Keys. This paper investigates the morphology, variation, and occurrence of growth forms, and the responses of this coralline alga to differing environmental conditions. Tavernier Key is an emergent back reef mound with a windward zonation of carbonate-producing communities. The windward shallow-subtidal and intertidal zones are dominated by the branching *N. strictum*. This facies is divided into three subfacies. A framework subfacies of *in situ*, branching *N. strictum* thalli occupies the sheltered shallow-subtidal areas. A rhodolith subfacies occurs in intertidal, moderately exposed parts of the mound. Rhodoliths are generated from collapsed sections of the framework and branches show increasing amounts of redirected growth as rhodoliths are transported shorewards away from the framework subfacies. Exposed areas on the north-east of the mound are characterized by a gravel patch subfacies. These gravel patches have clean, sandy gravels that migrate shorewards during storms over the muddy inshore *Thalassia* beds. The main palaeoecological conclusions arising from this work are the narrow depth range of the *Neogoniolithon* facies, the morphological response of this coralline to low-water level and hydraulic energy, and the preservation of growth forms and facies in rhodolith cores.

CORALLINE algae have been important agents in the formation of limestone since the Palaeozoic (Wray 1977). Their calcified skeletal tissue enables them to construct reefs (Ginsburg and Schroeder 1973; Bosence 1983*a*, 1984), rhodoliths (Bosellini and Ginsburg 1971; Bosence 1983*b*), and, on breakdown, coralline algal sands and gravels (Bosence 1980). In addition to their rock-forming capabilities, recent studies have shown that coralline algae are very useful palaeoenvironmental indicators for the Tertiary (Adey and MacIntyre 1973; Adey 1976; Bosence 1983*a*, *b*, *c*). This is a result of their strict environmental tolerances, morphological responses to hydraulic energy, and their slow rate of evolution. Similarly, the investigation of the ecology of Recent coralline algae aids in the interpretation of the abundant late Palaeozoic mound-building ancestral corallines (Wilson 1975).

This paper investigates the occurrence, ecology, and preservation of a Recent mound-building coralline alga *N. strictum* Setchell and Mason, 1943. *N. strictum* occurs as branching frameworks, rhodoliths, and mud to gravel-sized sediment. Growth forms are varied and, in particular, rhodolith morphology very closely reflects local environmental conditions. The conclusions from this work emphasize the sediment-building capabilities of coralline algae and their value in palaeoecological studies. *N. strictum* is common in many shallow water areas of the Caribbean (Foslie 1901; Setchell and Mason 1943; Adey and MacIntyre 1973; Enos and Perkins 1977; Adey pers. comm. 1984). In the Florida Keys it occurs commonly in back reef areas, on the seaward margins of carbonate mounds, and in tidal channel passes (Enos and Perkins 1977; Turmel and Swanson 1976). Adey (pers. comm. 1984) has reported a 3 km long fringing reef of *N. strictum* in a lagoon from Mayaguana, south-eastern Bahamas. The present study area of Tavernier Key is some 2 km east of southern Key Largo (text-fig. 1) and south-west of a similar mound (Rodriguez Key) described by Turmel and Swanson (1976). This paper forms part of a wider investigation to study the sediment production, deposition, and geological history of Tavernier Mound (Bosence *et al.* in press).

[Palaeontology, Vol. 28, Part 1, 1985, pp. 189–206, pls. 21–23.]



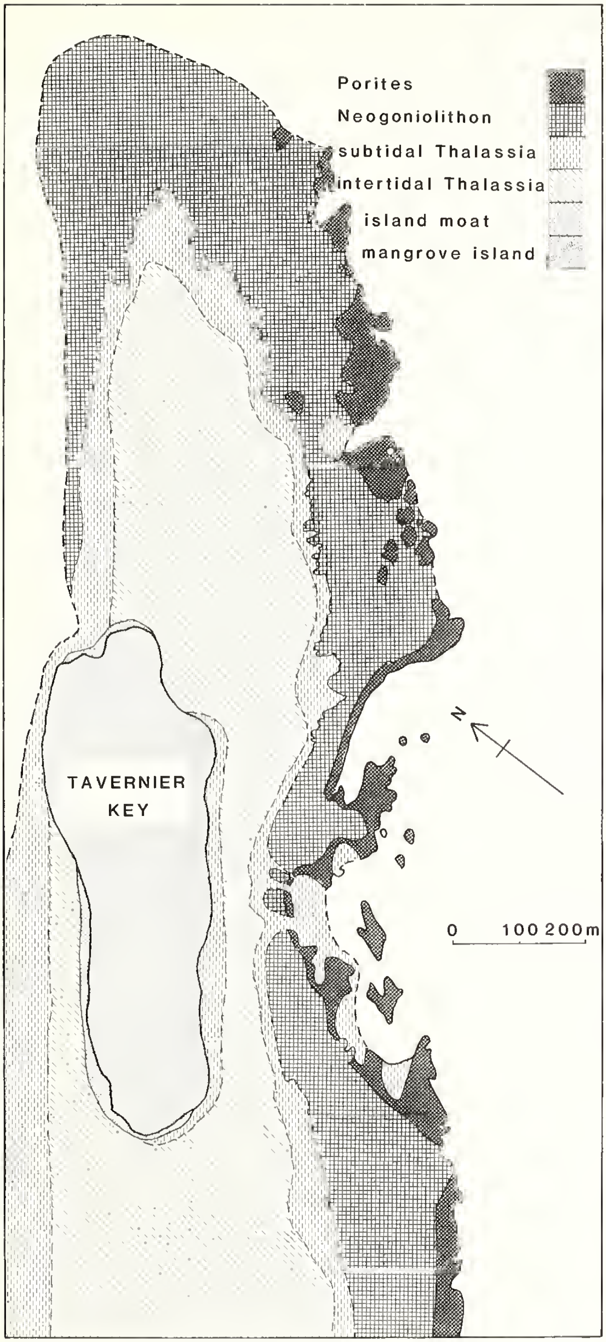
TEXT-FIG. 1. Location of Tavernier mound in the Florida Keys (after NOAA Chart 11451).

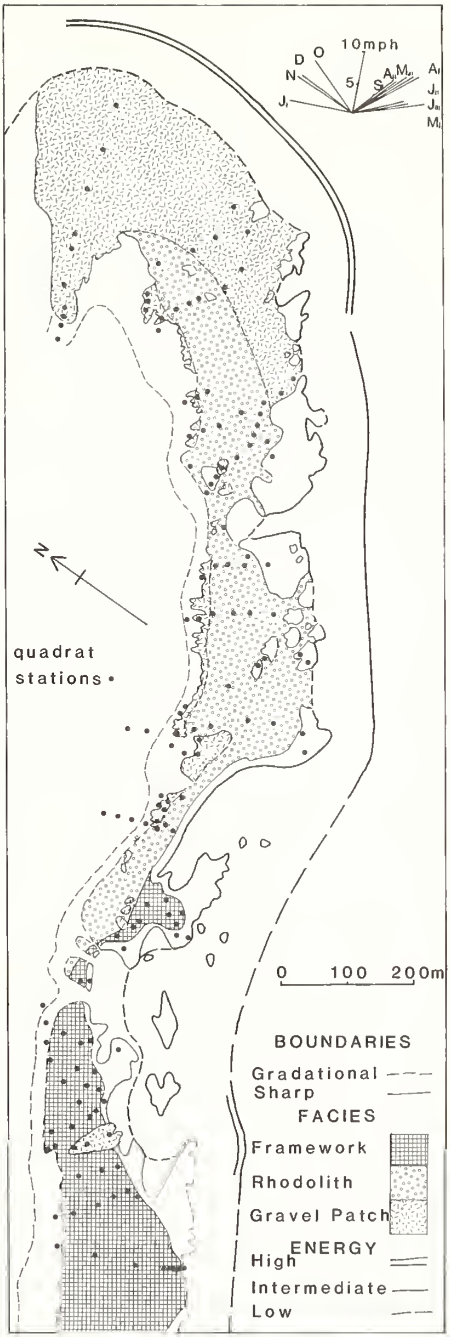
METHODS

Tavernier mound has been surveyed and mapped (text-figs. 2, 3) on a scale of 1 : 1500 using draughting film base maps prepared from low-altitude aerial photographs. Quadrat surveys (223 stations) were undertaken in February 1980 and August 1981 (text-fig. 3). Some 1,500 rhodoliths were collected, measured, and classified according to shape, branching density, and numbers of redirected branch growths. Shapes were estimated as being spheroidal, ellipsoidal, or discoidal. Branching densities were classified as single (I), occasional (II), common (III), or dense (IV) branching (Bosence 1976). Size was measured along the long (L), intermediate (I), and short (S) axes of rhodoliths and calculated using the volume of an ellipsoid ($\frac{4}{3}\pi$ LIS) (Bosence 1976, 1983*b*). Representative rhodoliths were impregnated and sectioned to study their internal structure; some were fractured, coated with gold, and studied with a JEOL 35 scanning electron microscope operating at 25 kV. Box cores were taken to study the shallow subsurface and over fifty piston cores to the Pleistocene rock basement were collected to investigate preservation of mound facies. Data- and word-processing were carried out on a BBC microcomputer. Figured hand specimens are housed in the Marine Algal Section (box collection, BM) in the Department of Botany, British Museum (Natural History).

ENVIRONMENTAL SETTING OF CORALLINE ALGA

Tavernier Key is a Holocene (6000 BP) carbonate sediment mound built up on a basement of lithified Pleistocene Key Largo Limestone of the Floridian Plateau (Enos and Perkins 1977). The mound rises


Porites
Neogoniolithon
subtidal Thalassia
intertidal Thalassia
island moat
mangrove island
TAVERNIER KEY
N
0 100 200m


10mph
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quadrat stations •
0 100 200m
BOUNDARIES
Gradational
Sharp
FACIES
Framework
Rhodolith
Gravel Patch
ENERGY
High
Intermediate
Low

TEXT-FIG. 2 (*left*). Sediment-biotic facies on Tavernier mound. The facies continue to the south-west of the map paralleling the mound margin (Pl. 21, fig. 1).

TEXT-FIG. 3 (*right*). Sample stations and distribution of subfacies within *Neogoniolithon* facies. Relative hydraulic energy levels were obtained from wave orthogonal study combined with exposure to strongest and most frequent winds. Wind chart indicates mean monthly direction from which wind blew (1963–1979) (NOAA 1980). The framework sub-facies continues as a parallel band to the south-eastern end of the mound.

steeply (Pl. 21, figs. 2, 3) from the surrounding 1·5–3·0 m deep sea-bed to a flat upper surface. The mound surface is largely intertidal with an emergent, central mangrove and cottonwood vegetated island (Pl. 21, fig. 1; text-fig. 2). Major currents around and on the mound are from wind-generated waves which are predominantly south-south-easterly in summer and northerly in winter (NOAA 1980). Wave refraction studies show that the windward margin of the mound can be divided into sections experiencing relatively high-energy (converging wave orthogonals and exposure to north-easterly winds), intermediate (parallel wave orthogonals), and low-energy areas (diverging wave orthogonals and shelter from north-easterly winds) (text-fig. 3). Waves of average height (0·5 m) are either reduced to very low amplitudes as they pass over the mound surface at high tide, or break within the intertidal zone. Storm and hurricane waves may, however, break on to the Key (Ball *et al.* 1967). Salinity (34–37‰) and temperature (15–32 °C) of the surrounding waters are assumed to be similar to those of the reef tract (Ginsburg 1956; Enos and Perkins 1977) but increased values probably occur in local ponded areas on the mound surface. Measured tidal ranges correlated with those at Tavernier Bridge show that low-water spring tides reach the edge of the flat-topped mound surface.

Mapping of sediments and carbonate-producing communities shows a depth related zonation (Pl. 21, figs. 1, 3; text-fig. 2) (cf. Rodriguez Bank—Turmel and Swanson 1976). The windward margin of the mound rises sharply from the surrounding *Thalassia*-covered sea floor, with slopes constructed from an *in situ* framework of branching *Porites divaricata* (Pl. 21, figs. 2, 3). This facies extends up to 0·5 m below mean low water (MLW) and gives way on the mound to the *Neogoniolithon* facies (Pl. 21, figs. 4–8; text-figs. 2, 3) which is the main subject of this paper. A small band of *Neogoniolithon* also occurs on the northern leeward side of the mound but this has not been studied in detail. The *Neogoniolithon* facies extends from 0·5 m below to 0·1 m above MLW. Shorewards the mound is covered with various *Thalassia*-dominated communities (Pl. 21, fig. 7; text-fig. 3). A deeper subtidal *Thalassia*-covered area passes shorewards into shallower, emergent *Thalassia* facies dominated by callianassid shrimp mounds. These *Thalassia* facies accumulate gravelly and sandy muds. A sand floored tidal channel surrounds the island which is fringed with mangrove swamps accumulating peat. The central part of the Key is constructed of gravel storm ridges.

GROWTH AND MORPHOLOGY OF *NEOGONIOLITHON STRICTUM*

Foslie (1901) described the typical subdichotomous and lower right-angled branching of this coralline alga; he also noted the curved tapering branches with rounded apices. Foslie gave branch cell measurements of 35–55 μm

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EXPLANATION OF PLATE 21

Fig. 1. Easterly aerial view of Tavernier mound and Key with southern tip of Key Largo visible in top right. Zonation of mound displayed by low-water spring tide and waves shoaling on dark *Porites* facies (p), *Thalassia* covered surrounding sea floor (s), *Neogoniolithon* facies (n), gravel patches (g), subtidal *Thalassia* (st), and intertidal *Thalassia* (it). Arrow indicates earlier colonized gravel patches.

Fig. 2. Underwater photograph of *Porites* facies showing slope of mound edge and framework of *P. divaricata*, ×1.

Fig. 3. North-westerly aerial view of windward margin of Tavernier mound (letters as for fig. 1); scale from white 30–40 cm propeller scours.

Fig. 4. Underwater photograph from junction between *Porites* and *Neogoniolithon* facies illustrating coral being overgrown by algal crusts and branches, ×1.

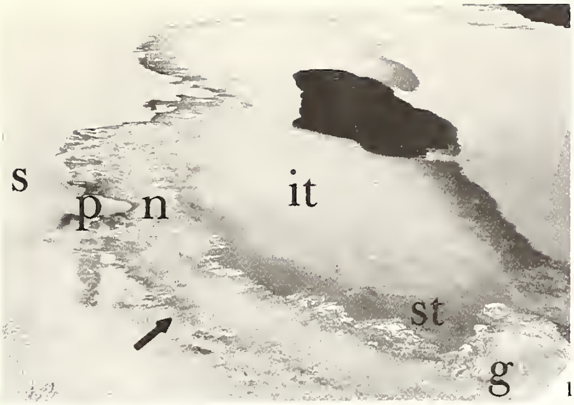
Fig. 5. Underwater photograph of lower part of *Neogoniolithon* facies with branching coralline overgrowing *Porites*; *Halimeda* and *Thalassia* blades to right, ×1.

Fig. 6. Underwater photograph of *Neogoniolithon* framework with intergrowing *Thalassia*; note flat-topped framework typical of thalli from the low-water level, ×0·25.

Fig. 7. Occasional large stabilized rhodoliths occur in the subtidal *Thalassia* beds inshore from the *Neogoniolithon* facies, ×0·5.

Fig. 8. Margin of intertidal pond in *Neogoniolithon* facies showing range of growth forms from the subtidal (right) to the intertidal (left); isolated domed heads in the subtidal become flat topped and grow sideways to merge with neighbouring thalli at the low-tide level (shovel 30 cm wide).

PLATE 21



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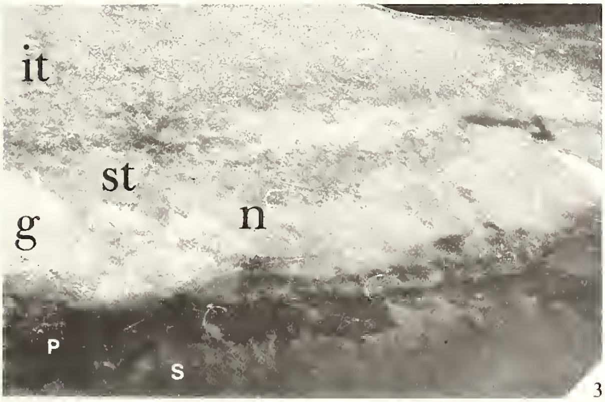

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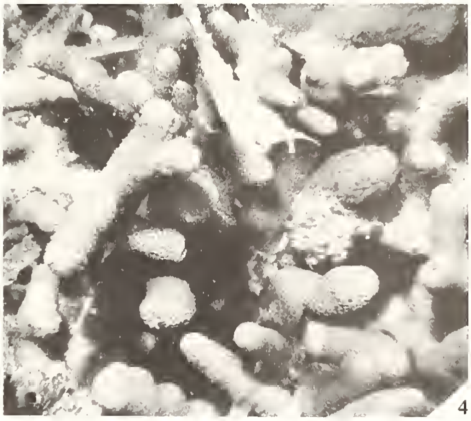

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BOSENCE, Tavernier mound, Florida Keys

long and 15–25 μm broad for medullary cells, and less regular square to rounded cortical cells measuring 15–25 μm long and 15–20 μm wide; he also noted the common large heterocysts. Foslie's material was sterile and the reproductive structures have not been described (empty unipored conceptacles are illustrated in text-fig. 4E). Setchell and Mason (1943) discussed the nomenclatural problems of Foslie's *Goniolithon* and erected a new genus, *Neogoniolithon*, which included the former *G. strictum*.

N. strictum encrusts any available hard substrate in the shallow windward edge of Tavernier mound. Crusts are 170–350 μm thick (mean 288 μm, standard deviation 55 μm) and are closely applied to the substrate. The hypothallus is not well developed but when present is coaxial, one to three horizontal cells thick with rectangular cells 30–40 μm long (mean 37 μm, standard deviation 3 μm) and 11–17 μm wide (mean 13 μm, standard deviation 2 μm) (text-fig. 4C, G). The perithallus is an irregular grid (text-fig. 4C) with subsquare cells 8–24 μm long (mean 17 μm, standard deviation 5 μm) and 8–28 μm wide (mean 16 μm, standard deviation 5 μm). Heterocysts are common and are formed of one to three vertically stacked, rectangular to arched cells, the largest of each group measuring 29–40 μm high (mean 34 μm, standard deviation 6 μm) and 25–35 μm wide (mean 29 μm, standard deviation 3 μm) (text-fig. 4C, H).

The commonest growth form of *N. strictum* is branched thalli that arise from crusts (Pl. 22). Their characteristic tapered branches result in variable branch diameters from 1·3 mm in young branches to 3·5 mm in old branches. Branches have a wide, central unzoned medulla with coaxial rectangular cells (text-fig. 4B, F), 24–42 μm long (mean 33 μm, standard deviation 5 μm) and 13–20 μm wide (mean 18 μm, standard deviation 2 μm). The outer cortex is of variable width and composed of smaller, subsquare cells with a similar cell size to those of the perithallus in crusts. The tapering branches are thickened by 60–100 μm thick sheaths of cortical tissue growing up to the branch tip (text-fig. 4B). As far as I am aware this mode of branch growth has not been described in corallines previously. The common form of branch width growth is an outward growth of cortical tissue by the lateral meristem (Cabioch 1972).

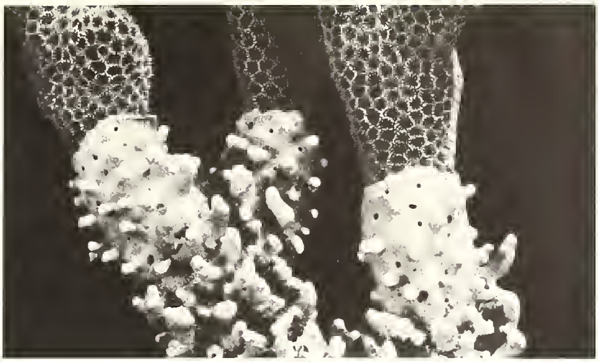
Two main processes in branch formation have been observed. Pseudodichotomous apical branching gives rise to branches diverging at low angles from each other (mean angle of divergence 41°, standard deviation 13°) (Pl. 22, fig. 5). In this case the central medullary region divides into two equal sections. Occasionally repeated apical branching occurs in one plane, giving rise to a fan-like branch arrangement (Pl. 22, fig. 5). Lateral branching results from rejuvenation of the lateral meristem and gives rise to branches that diverge at right angles to one another (mean angle of divergence 80°, standard deviation 12°) (Pl. 23, fig. 4). Similar branching types were illustrated for *Goniolithon* (*Neogoniolithon*) by Cabioch (1972), and *Phymatolithon calcareum* and *Lithothamnium corallioides* by Bosence (1976).

FRAMEWORKS, RHODOLITHS, AND SEDIMENTS OF THE *NEOGONIOLITHON* FACIES

Neogoniolithon occurs in an elongate facies on the windward margin of the mound (Pl. 21, fig. 1; text-figs. 2, 3). The facies can be divided into three subfacies based on the growth forms of *N. strictum* and sediment characteristics: framework subfacies, rhodolith subfacies, and gravel patch subfacies (text-fig. 3).

EXPLANATION OF PLATE 22

Figs. 1–7. *Neogoniolithon strictum* Setchell and Mason, 1943. 1, BM 1630, live *Porites* being overgrown upwards by crusts and branches of *N. strictum*; crusts and branches later bored by sponge, × 1·5. 2, BM 1631, *Porites* branch completely overgrown by *N. strictum* to form dome-shaped thallus typical of the shallow subtidal zone, × 1. 3, BM 1632, discoidal rhodolith arising from overgrowth of branched *Porites*; two growth directions are preserved, × 2. 4, BM 1633, fragment of framework derived from earlier collapsed segment; note lateral branching (arrowed) with redirected growth, × 0.75. 5, BM 1634, ellipsoidal rhodolith with pseudodichotomous branching (arrowed) which may be repeated in one plane to produce fan-like branches, × 1. 6, BM 1635, underside of framework illustrating extensive bioerosion of thallus, × 1·5. 7, BM 1636, rhodolith illustrating effects of turning on growth: (i) vertical *Porites* fragment in framework, (ii) branching framework growth of *N. strictum* (to left of figure), (iii) turning and redirected vertical growth (up figure), (iv) turning and redirected present-day growth (out of figure); note also nestling *Barbatia* in rhodolith core, × 0·75.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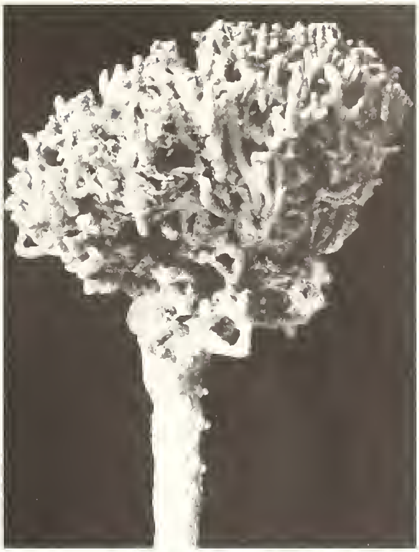
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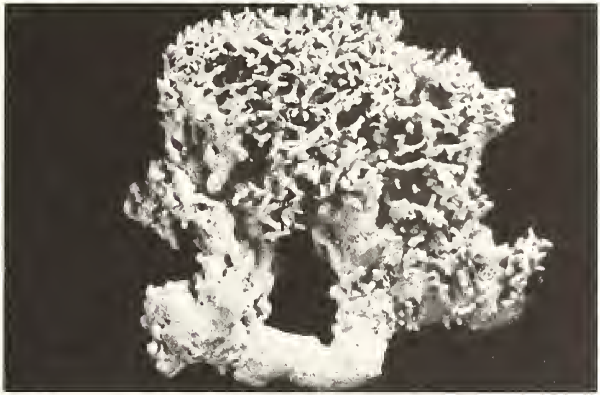
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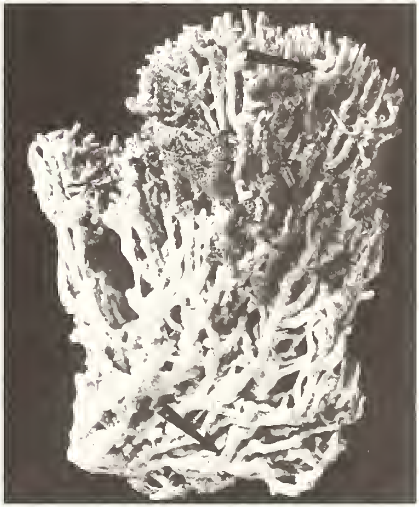
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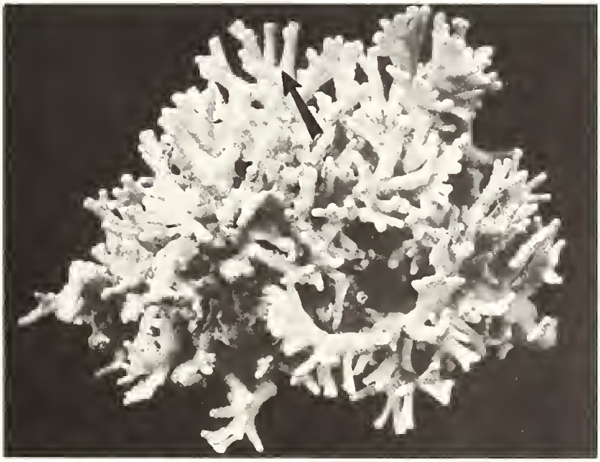
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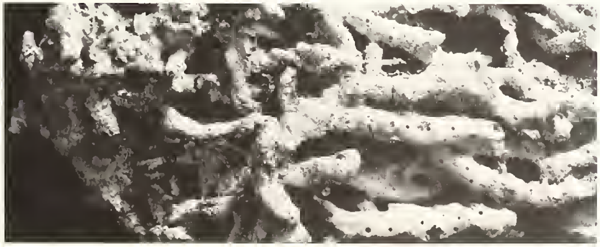
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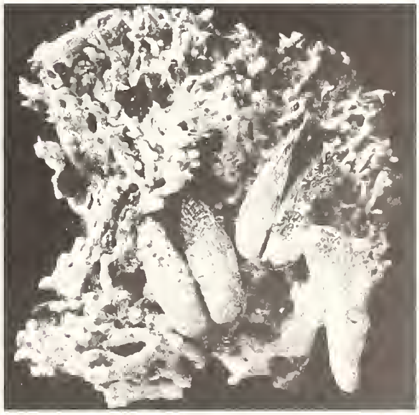
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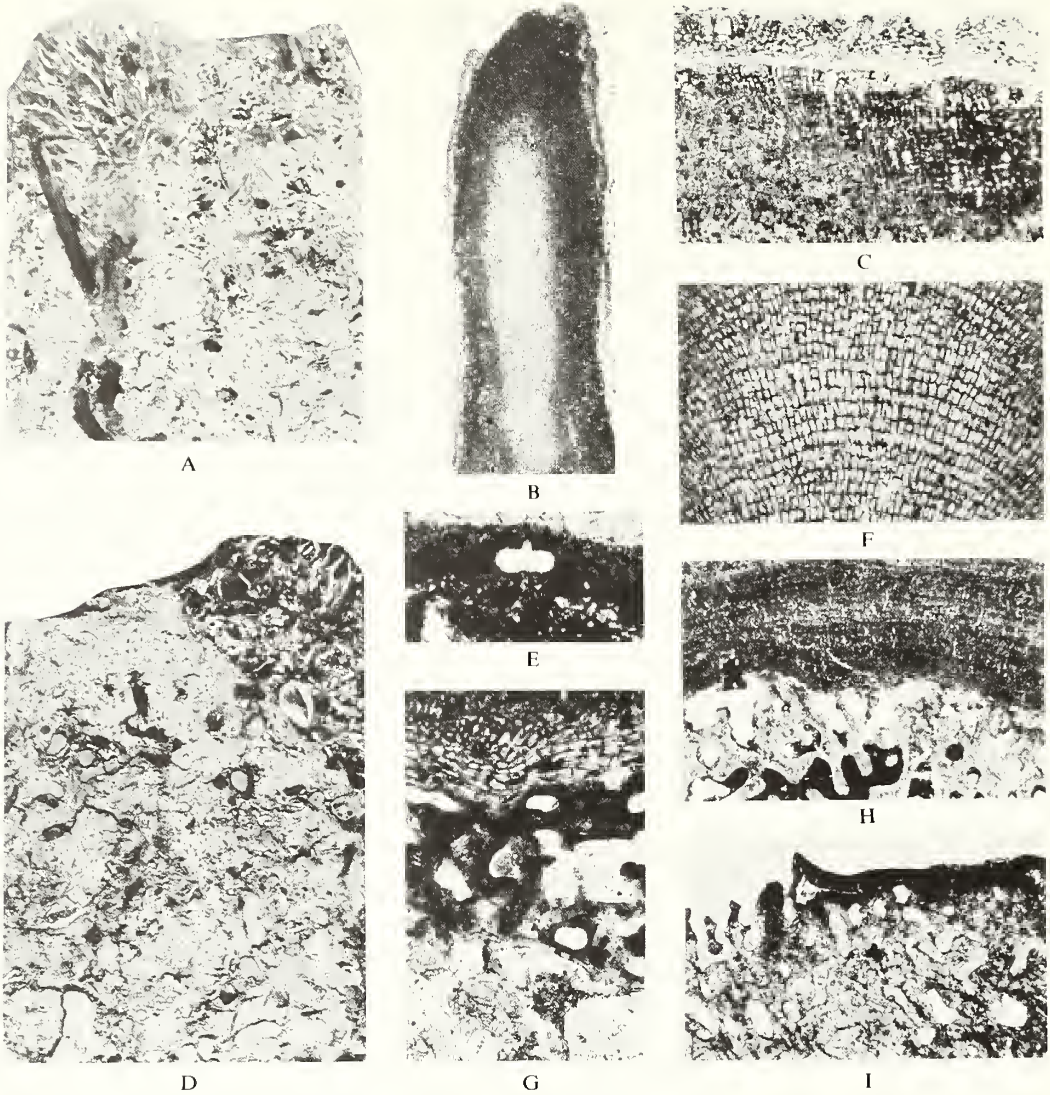
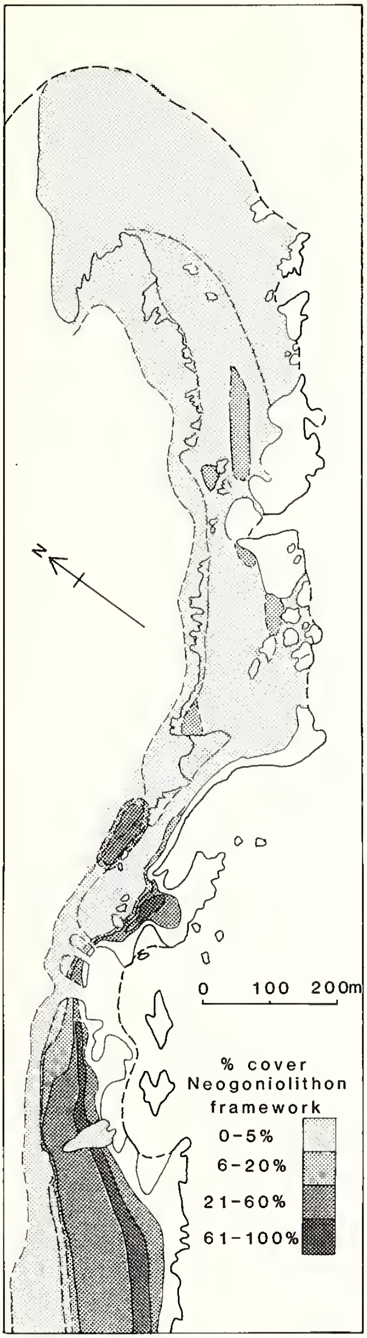
BOSENCE, *Neogoniolithon*



TEXT-FIG. 4. A, impregnated box core illustrating *Neogoniolithon* framework and lower burrowed gravel; note *Thalassia* roots and rhizome in upper part of core, and *Porites* branches at the base, ×0·25. B, longitudinal section of *N. strictum* branch illustrating inner medullary tissue and outer cortical tissue with heterocysts; note outer crustose sheath overgrowing branch, ×10. C, detail of B illustrating inner partially micritized cortical tissue, with vertically arranged heterocysts overgrown by new crust with one to three cell thick hypothallus, ×60. D, impregnated box core illustrating *Neogoniolithon* framework with *in situ Codakia*, lower burrowed muddy gravel with *Porites* and rhodolith, ×0·25. E, empty unipored conceptacle of *N. strictum*, ×30. F, detail of B with coaxial unzoned medullary tissue from branch centre, ×60. G, lower *Porites* bored by sponges (spicules lower left) and fungae overgrown by crust of *N. strictum*, ×60. H, lower fresh *Porites* overgrown by crust of *N. strictum* indicating overgrowth of live *Porites*, ×60. I, *N. strictum* crust overgrowing dead fungal-bored *Porites*, ×60.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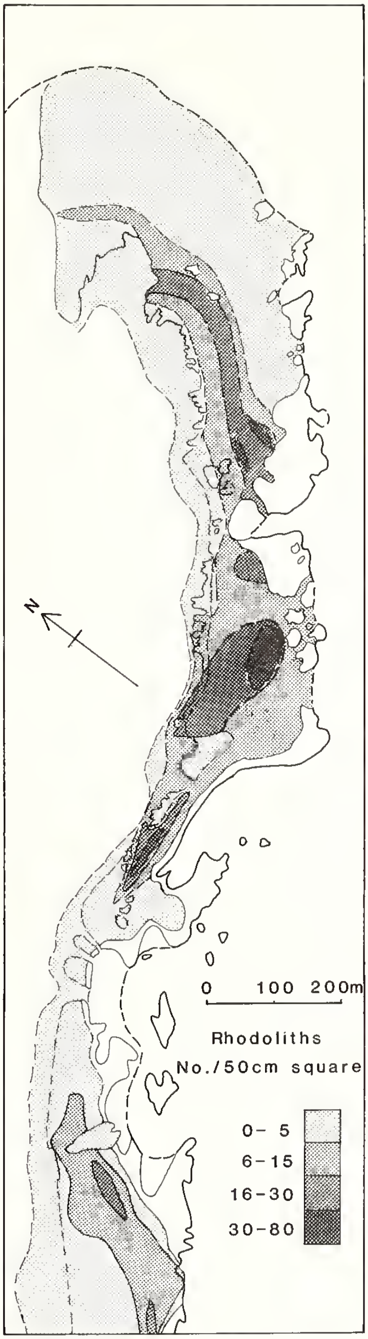
0 100 200m
% cover
Neogoniolithon
framework
0-5%
6-20%
21-60%
61-100%


N
0 100 200m
Rhodoliths
No./50cm square
0- 5
6-15
16-30
30-80

TEXT-FIG. 5 (*left*). Abundance (estimated as percentage quadrat cover) of *Neogoniolithon* framework at sample stations shown in text-fig. 3.

TEXT-FIG. 6 (*right*). Abundance of rhodoliths (number per 50 cm square) at sample stations shown in text-fig. 3.

Framework subfacies

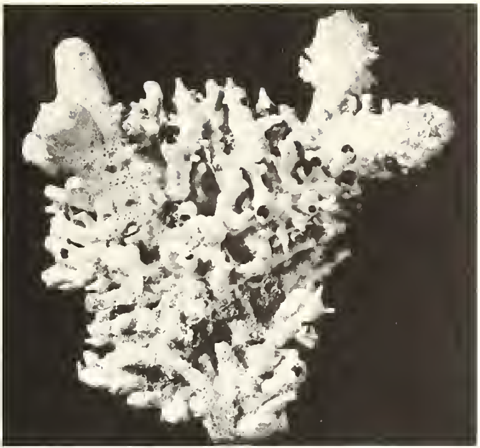
This subfacies is characterized by an *in situ* framework of *N. strictum* (text-figs. 3, 5; Pl. 21, fig. 5) covering an average 45% of the sea floor. *Porites* frameworks may persist in shallow subtidal areas with an average cover of 10%. Frameworks have a relief above the sedimentation level of up to 15 cm and extend into the shallow subsurface (text-fig. 4A, D). Sediment around the frameworks is a muddy sandy *Neogoniolithon* gravel which gives way to muddy *Neogoniolithon* gravel in the sheltered near-shore areas. The gravels are composed mainly of *N. strictum* (69%) with lesser amounts of *Halimeda* (17%), mollusc (7%), *Porites* (4%), and foraminifera (1%). *Thalassia* cover over the framework is commonly 40–50%. Text-fig. 5 illustrates the percentage cover of *Neogoniolithon* framework. The major concentrations occur in the more sheltered southern parts of the mound (cf. text-fig. 3). In addition, the framework occurs in small amounts on the windward margin of the rhodolith sub-facies adjacent to the *Porites* facies.

Shallow subtidal areas of the *Porites* facies illustrate the main way in which the *Neogoniolithon* framework is formed. Fresh crusts of *N. strictum* are found on the lower dead branches of *Porites* (Pl. 21, fig. 4). These crusts grow marginally and eventually overgrow the live upper parts of the *Porites* branches, killing off the live coral (Pl. 21, figs. 4, 5; Pl. 22, fig. 1). This can be seen in sections from live specimens, or preserved in dead specimens where crusts overgrow fresh unbored coral surfaces (text-fig. 4H). Conversely, overgrowth of dead surfaces is characterized by algal and fungal borings (text-fig. 4G, I). Branches arising from these crusts grow upwards, thicken, and rebranch to eventually form a dense interlocking framework. Branches may fuse together with the growth of additional cortical tissue. Growth begins as rounded isolated heads (Pl. 22, fig. 2); adjacent heads then coalesce to form a continuous framework. Within the framework are many nestling and crevice-dwelling bivalves (*Brachidontes*, *Barbatia*, and *Crassostrea*; Pl. 22, fig. 7; Pl. 23, fig. 3), gastropods (*Vermetus* and *Ceritheum*; Pl. 23, fig. 1), echinoids (*Echinometra* and *Diadema*), ophiuroids, crustaceans (shrimps, stone crabs, lobsters, and hermit crabs), encrusting serpulids, bryozoans, and foraminifera. The framework is commonly overgrown by sponges (*Haliclona*, *Timea*, and *Spongia*) and tunicates (*Ascidea*).

Framework growth continues to the low-water spring-tide level where upward growth is halted and the framework has a flatter top and is more densely branched (Pl. 21, fig. 6). Depressions in the mound surface are ponded at low-water spring tides with a constant tide level. Here adjacent growth heads have a common flat top and the margins of plants have large overhangs as subsequent growth is by lateral branching lower in the thallus (Pl. 21, fig. 8). The restricted upward growth and increased lateral branching results in adjacent heads coalescing with a common flat top. In this way the framework may cover up to 90% of the mound surface. Only the upper few centimetres of the framework is alive, below which occurs a band of bioerosion by sponges, algae, and fungi (Pl. 22, fig. 6). Beneath this dead zone, which is of variable height, the framework is buried by a muddy sandy *Neogoniolithon* gravel (text-fig. 4A, D). Box cores illustrate the *in situ* preservation of the framework in the shallow subsurface, but at 10–20 cm below the level of sedimentation the framework is lost, as is its original substrate. Similarly, piston cores through the mound do not penetrate areas of framework in the subsurface. There is clear evidence of the framework being weakened by small-scale bioerosion.

EXPLANATION OF PLATE 23

Figs. 1–8. *Neogoniolithon strictum* Setchell and Mason, 1943. 1, BM 1637, discoidal III rhodolith arising from branching *Porites*; note intergrown vermetid gastropods in coralline branches, × 1. 2, BM 1638, ellipsoidal III rhodolith illustrating two directions of growth and great variation in branch thickness, × 1. 3, BM 1639, rhodolith with nestling *Ostrea* and *Barbatia* later overgrown by coralline, × 1. 4, BM 1640, discoidal III rhodolith illustrating two main directions of growth, × 1. 5, BM 1641, spheroidal III rhodolith, × 1. 6, BM 1642, ellipsoidal II rhodolith illustrating two main directions of growth, × 1·5. 7, BM 1643, ellipsoidal III rhodolith illustrating three directions of growth (vertical, left to right, and out of figure), × 1. 8, BM 1644, rhodolith with columnar growth and severe echinoid grazing marks over surface, × 1.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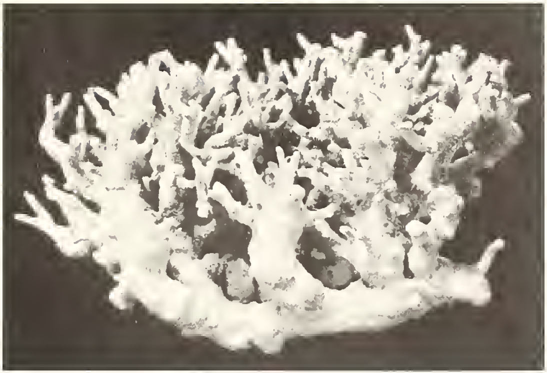
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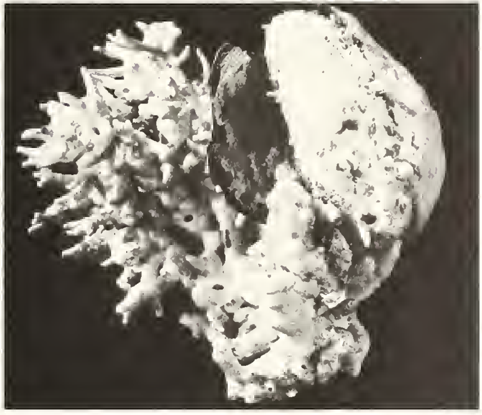
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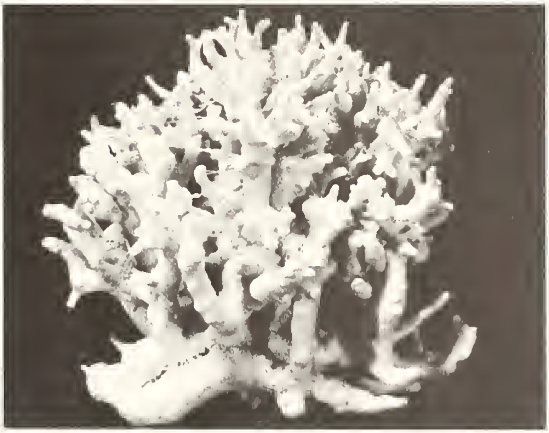
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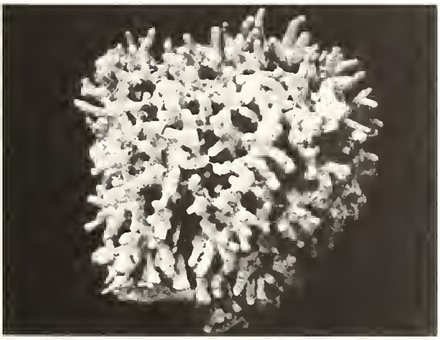
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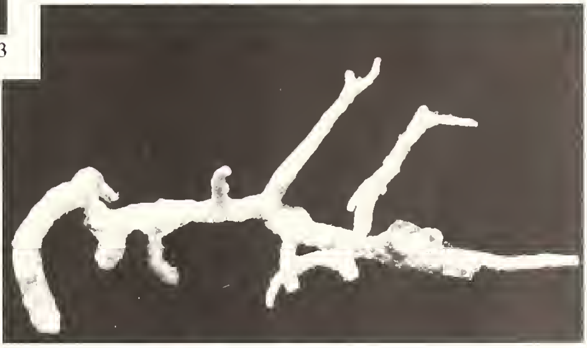
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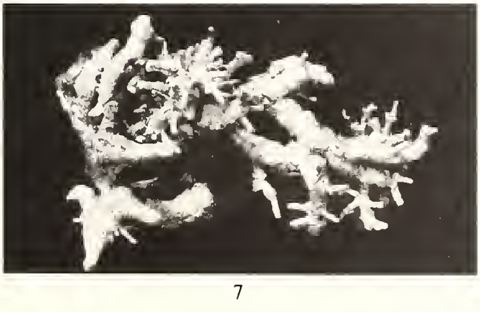
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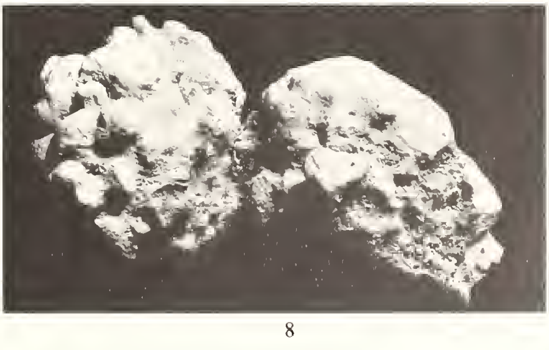
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BOSENCE, *Neogoniolithon*

No evidence for dissolution has been seen under the SEM. The most likely cause for the final breakup of the framework is the burrowing of crabs, lobsters, and shrimps (*Callianassa major*). These crustaceans are abundant on the mound and debris from their burrows shows freshly broken algal, coral, and molluscan skeletons. Box cores show burrows and bioturbation textures that could have been produced by these crustaceans. Therefore, although the framework is abundant on the mound surface and shallow subsurface, it is destroyed by bioerosion and burrowing to form mud, sand, and gravel-sized debris. These sediments are abundant over the entire surface of the present-day mound and to depths of 2 m in the subsurface.

Rhodoliths are generated from the framework by the breakage of branching segments. After falling on to the substrate, growth is either redirected vertically or new lateral branches arise from the upper surface (Pl. 22, figs. 3, 4, 7). When turned again, these rhodoliths may record a new growth direction and thus give an indication of the amount of movement involved. Rhodoliths from the framework subfacies are characterized by having only two directions of branch growth (text-fig. 8). Rhodoliths are most commonly ellipsoidal in shape (59%), less frequently discoidal (32%), while spheroidal shapes (10%) are the least abundant. Rhodoliths are common (average eight per 50 cm square) and are larger (40 cm^3) than those occurring in other subfacies on the mound.

Rhodolith subfacies

This subfacies is characterized by an abundance of rhodoliths (averaging eighteen per 50 cm square; range five to ninety), sandy *Neogoniolithon* gravels, a *Thalassia* cover averaging 34%, and small patches of *Neogoniolithon* frameworks (2%). The subfacies occurs mainly to the north of the framework subfacies in the more exposed part of the mound (text-figs. 3, 6). Sediments are poorly to very poorly sorted and composed mainly of *Neogoniolithon* (68%), with lesser amounts of *Halimeda* (15%), molluscs (7%), *Porites* (6%), and foraminifera (2%). Rhodoliths are commonest in the central to windward part of the subfacies (text-fig. 6). Numbers decrease into the shoreward *Thalassia* beds where the sediments are muddier. Similarly, abundance decreases in the highest energy area of the north-eastern end of the mound. Rhodoliths are therefore most abundant in areas of intermediate hydraulic energy. Nearly all rhodoliths are of close-branching morphology and many are derived from segments of branching frameworks that have been turned so that growth is redirected (Pl. 22, fig. 7). Other rhodoliths start from *Porites* sticks (Pl. 22, fig. 3; Pl. 23, fig. 6), *Siderastrea* colonies, bivalve shells, gastropods, or artificial substrates. Initial growth on these substrates is a crust that gives rise to upward-growing branches. With occasional turning, growth is redirected (Pl. 23, figs. 2, 4). Occasional rhodoliths are found with a columnar construction. These are always found on a sandy gravel or gravel substrate. The surface of these rhodoliths is usually scoured by echinoid grazing traces (Pl. 23, fig. 8).

Rhodoliths are mainly ellipsoidal (64%) and this shape is often seen to have originated from an elongate section of *Neogoniolithon* framework. Discoidal shapes are the next most common (29%) and these are often formed from an elongate branch which has redirected its growth along one edge only. Others derive their shape from mollusc shells or *Porites* sticks with branches in one plane (Pl. 22, fig. 3; Pl. 23, fig. 1). Spheroidal rhodoliths are the least common (7%) and are characteristically densely branched (Pl. 23, fig. 5). Branching densities of rhodoliths from this subfacies are most commonly 'frequent' (70%) and least commonly 'occasional' (15%) and 'dense' (15%). The number of growth directions recognizable in rhodoliths is commonly two (33%) (Pl. 23, fig. 2), three (28%) (Pl. 23, fig. 7), or four (17%) (Pl. 22, fig. 7). This shows increased turning and transport compared with rhodoliths from the framework subfacies (text-fig. 8). Rhodoliths are slightly smaller (36 cm^3) than those from the framework subfacies which suggests some breakage with transport (text-fig. 8).

Gravel patch subfacies

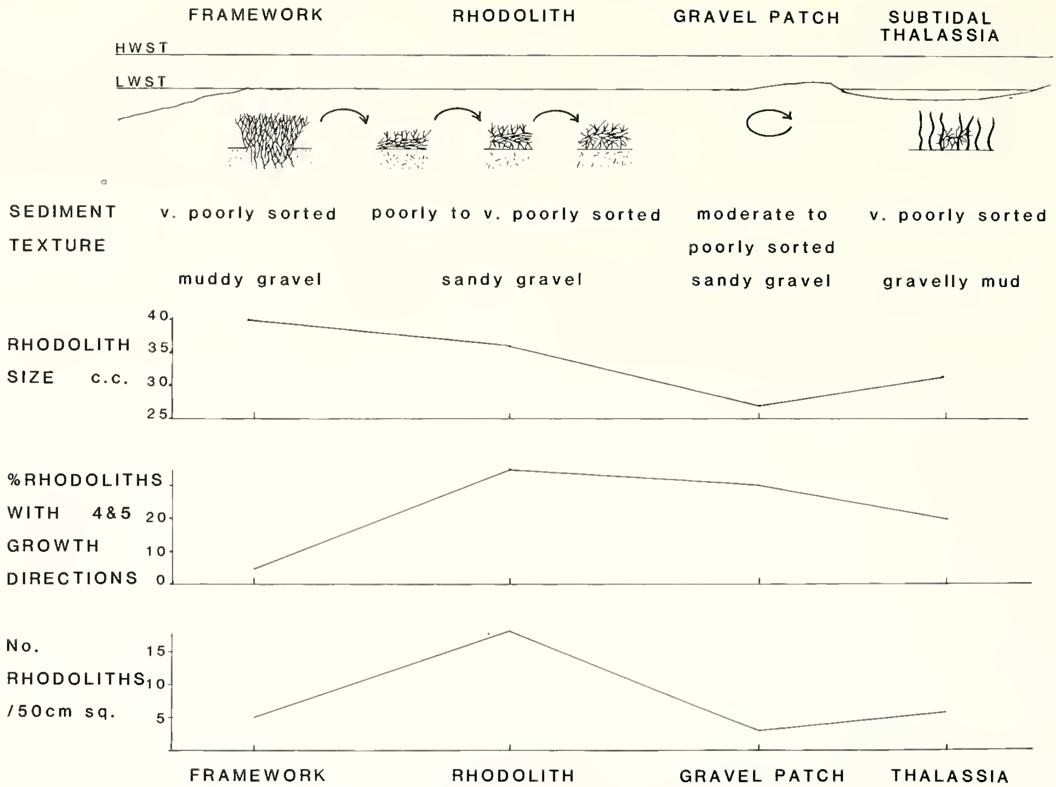
Oblong patches of sandy gravel or gravelly sand occur with their long axes normal to the mound edge. The patches have no coralline framework, a thin *Thalassia* cover (14%), and few rhodoliths (three per 50 cm square). Most patches of coralline gravel occur within the rhodolith subfacies, with a particularly large area to the north of the mound. In the south, however, a large patch cuts across the framework subfacies. The gravel patches occur in locations with the highest wave energy on the mound where wave orthogonals converge (text-fig. 3). Their long axes are orientated parallel to the direction of refracted wave approach. Sediments on the patches are moderately to very poorly sorted and of similar composition to those previously discussed (*Neogoniolithon* 62%, mollusc 14%, *Halimeda* 13%, *Porites* 4%, and foraminifera 0·5%).

Sediment is transported shorewards along the gravel patches by breaking waves. The central area of each patch may be slightly scoured and rippled, and at the shoreward crest of the patch a 10–15 cm face of gravel avalanches down into the near-shore *Thalassia* beds. The gravel patches thus mark the shoreward edge of the *Neogoniolithon* facies (Pl. 21, fig. 1). As the patches move shoreward, the seaward margin begins to be colonized by macrophytes in the following successional order: *Penicillus–Syringodium–Thalassia*, and finally an increase in *Neogoniolithon* rhodoliths. A short visit to Tavernier mound in August 1983 showed that previously mobile gravel patches seen in August 1982 (following tropical storm Dennis) had become stabilized by plants and their margins were less sharp. Old stabilized gravel patches are now preserved as bands of *Thalassia*-rich and *Thalassia*-poor areas within the rhodolith sub-facies of the northern mound (Pl. 21, fig. 1). Rhodoliths in the patches are rather scarce compared to their abundance on either side, behind, and on the front avalanche face of the patches (text-fig. 7). This is thought to be due to their rapid transport over the patches. Branching densities and numbers of growth directions of rhodoliths from the patches is similar to those from the rhodolith subfacies. This also suggests that transport is too rapid for the rhodoliths to show any growth response to the new conditions. The small size of the rhodoliths (27 cm^3) suggests that some abrasion occurs with transport.

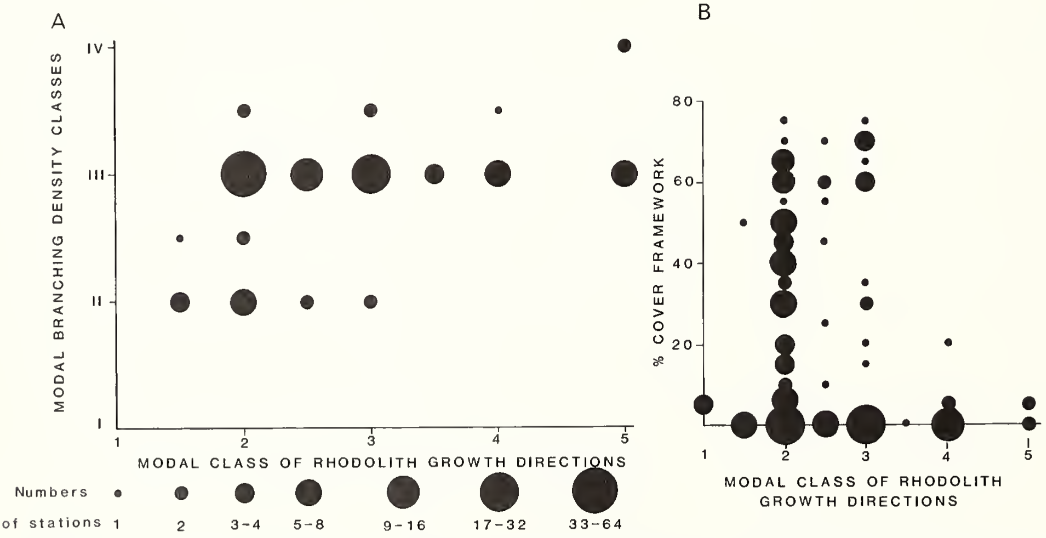
Summary and discussion

The shallow seaward margin of Tavernier mound is dominated by the branching coralline alga *N. strictum*. In shallow subtidal areas *N. strictum* overgrows *Porites*, and in sheltered parts of the mound it forms a dense branching framework up to low-tide level. Vertical growth is restricted in the intertidal zone and bushy thalli grow sideways to merge with neighbouring clumps; these clumps have a common flat top at low-water spring-tide level. The framework is weakened by bioerosion and segments are broken off to continue life as rhodoliths in the areas of intermediate wave energy on the mound (text-fig. 7). With shoreward transport, the rhodoliths are turned and growth is redirected so that two or more branch growth directions can be recognized (text-fig. 7). Eventually rhodoliths may take on their more typical radial growth habit. The majority of rhodoliths are of class III (common) branching density but classes I, II, and IV also occur. If modal classes of branching density for each station are compared with numbers of growth directions within the rhodoliths, a positive correlation can be seen (text-fig. 8). Previous workers have shown that increased branching density is a response to increased transport and apical abrasion (Bosellini and Ginsburg 1971; Bosence 1976, 1983*b*, *c*). This is also suggested here, with the evidence for increased transport being preserved in the lateral branching and new growth directions. One other source can be found for densely branched rhodoliths on Tavernier mound. Stations from the windward edge of the *Neogoniolithon* facies contain small numbers of densely branched rhodoliths. These rhodoliths, however, have a small number of growth directions and their close proximity to dense frameworks at the low-tide level suggests a local derivation. The occurrence of rhodoliths and their numbers of growth directions is shown in text-fig. 7. From this it can be seen that the areas of framework subfacies have rhodoliths with few growth directions (two or three) whilst areas of the rhodolith subfacies and gravel patch subfacies have higher numbers of growth directions, again indicating transport away from the frameworks. Similarly, a negative correlation exists between percentage cover of *Neogoniolithon* framework and numbers of growth directions within rhodoliths (text-fig. 8B), suggesting transport of rhodoliths away from frameworks.

The preservation of distinct growth directions within rhodoliths suggests fairly long periods (several years) when they are stationary, interrupted by a period or periods of transport. Transport is thought to be mainly by storms as normal wave conditions do not move rhodoliths. Observations immediately after 80 km.p.h. winds of tropical storm Dennis (August 1982) showed turned and



TEXT-FIG. 7. Summary of variation in morphology of *Neogoniolithon strictum* across subfacies on the mound surface (data from 1,500 rhodoliths from 220 stations, averaged for each subfacies).



TEXT-FIG. 8. A, modal branching density and modal growth directions of rhodoliths from stations on Tavernier mound; stations with denser branching rhodoliths also have rhodoliths with more growth directions. B, relationship between percentage cover of *Neogoniolithon* framework and number of growth directions of rhodoliths; stations with many growth directions have little *Neogoniolithon* framework (data from 1,500 rhodoliths from 220 stations).

transported rhodoliths (live, red-side down). Transport across the gravel patches is thought to be faster and is reflected in a reduction in rhodolith size. Some rhodoliths occur within the inner *Thalassia* beds. These are heavily infested with epiphytes and epizoans and are considerably weakened by bioerosion. Sediments have a similar composition throughout the three subfacies suggesting derivation from similar communities together with transport of grains over the mound surface. The only variation is in texture, which varies from the more poorly sorted and muddier sediments of the lower energy framework subfacies to the coarser better sorted gravels of the gravel patches.

COMPARISONS AND PALAEOECOLOGICAL CONCLUSIONS

Comparisons with Recent examples

N. strictum is found in environments similar to those on Tavernier mound in other areas of the Florida Keys. Turmel and Swanson (1976) have described a similar low-tide level, windward fringe of *N. strictum* on Rodriguez Bank, just to the north-east of Tavernier Key. A brief visit in 1981 confirmed their observations but there was not the same differentiation into subfacies as on Tavernier mound, and growth was less luxuriant. Other examples are known on sediment banks and channel margins from the back reef area of the Florida Keys (Enos and Perkins 1977). In all cases the environment is back reef, protected from the main ocean swell but exposed to local waves and/or tidal currents. Outside the Florida Keys, Adey (pers. comm. 1984) has observed similar occurrences at Mayaguana in the Bahamas. Here a 3 km, 0–2 m deep fringe is found in a lagoon experiencing increased temperatures (30 °C) and salinities (38‰). Therefore the branching framework of *N. strictum* is found in back reef or lagoonal environments, on a soft substrate, and within a metre or so of mean low water.

Other examples of *Neogoniolithon* reef frameworks are from the Mediterranean where a 'trottoir' or pavement occurs in the intertidal zone. The leafy crustose species *N. notarisii* can be either a component of a mixed coralline community constructing the 'trottoir' (Pérès and Picard 1964), or ledges, algal ridges, and microatolls may be constructed entirely by this alga (Thornton *et al.* 1978; Denizot *et al.* 1981). These reefs grow up to the intertidal zone where vertical growth is halted, lateral growth becomes important, and flat tops and overhangs develop. This is a similar response to the intertidal emergence of *N. strictum* on Tavernier mound where flat-topped and sideways-spreading clumps occur at the low-tide level. On a larger scale, coralline algal patch reefs (Ginsburg and Schroeder 1973; Adey 1975; Bosence 1984) and Pacific algal ridges (Emery *et al.* 1954) also show a similar growth response to sea level.

The branching framework of *N. strictum* may be considered intermediate in its construction between the thicker branched and early cemented branching frameworks of coralline algal ridges, and the unattached and uncemented branching frameworks of the temperate mearl (Bosence 1983*a*). The absence of early cementation in the *N. strictum* framework means that it is susceptible to breakage following bioerosion. Fracturing by waves and burrowing crustaceans reduces the preservation potential of the framework but leads to the formation of the associated rhodolith and gravel-patch subfacies.

Rhodoliths of *N. strictum* have not been described before but they can be compared with other detailed descriptions of rhodolith formation. Bosellini and Ginsburg (1971) described the morphological changes which take place as rhodoliths are transported from sea grass beds to channels in Whalebone Bay, Bermuda. Bosence (1976) analysed the variation in rhodolith morphology in temperate mearl beds of western Ireland. In neither of these two cases is there a similar area to that on Tavernier mound, where an *in situ* framework generates fragments to form rhodoliths. In all cases, however, a similar relationship exists between transport and branch morphology. Cessation of apical growth following abrasion leads to the growth of lateral branches and more densely branched rhodoliths. Redirected growth as a response to turning is most clearly seen in the Tavernier rhodoliths because of their derivation from the upward-branching frameworks. In ancient sequences the only evidence for the presence of former frameworks may be in the form of these unidirectionally branched rhodolith cores. It might be expected that coralline algal patch reefs would be surrounded by rhodoliths derived from fractured frameworks, but this has not been reported (Ginsburg and Schroeder 1973). Rhodoliths occurring around patch reefs in St. Croix have crustose growths of *Tenarea*, *Porolithon*, *Neogoniolithon*, and *Homotrema* over a core of coral, shell, or pebble (Adey 1975; Bosence 1984). They are clearly not derived from the reefs that have frameworks of branching and columnar *Lithophyllum* and *Porolithon*. The reason for this apparent anomaly is probably that the coralline patch reefs are rigid and well cemented, and the greatest agents of erosion are boring organisms. These organisms release fine-grained dead material often into an environment which is not conducive to the growth of reef-building corallines.

Comparisons with ancient examples

The pattern of framework, rhodolith, and gravel-patch formation on Tavernier mound (text-fig. 7), and the leeward change to rhodoliths showing increasing amounts of transport to leeward gravels, should be preserved in ancient sequences (see below). This pattern may be applicable to and aid in the interpretation of Miocene coralgal reefs from Israel (Buchbinder 1975). Here reef crests have branching frameworks of *L. prelichenoides* and *L. ghorabi*. Back-reef areas are rich in branching and crustose coralline debris of the same taxa. Buchbinder (1975) suggested that the abundance of debris is due to the presence of former branching frameworks on the back-reef platform area. A more complete picture results when this is compared with the Tavernier mound pattern. Branching debris can be related to framework breakdown and rhodolith formation and breakdown along the same transport path.

The Miocene Coralline Algal Biostrome of Malta (Bosence and Pedley 1982) also illustrates the relationship between framework, rhodoliths, and gravel, but in a deeper water setting. Crustose frameworks occur with branches arising from crusts. Within the frameworks are erosion surfaces, frequently lined with rhodoliths. The internal structure of the rhodoliths illustrates a framework-derived core with later fresh overgrowths of concentric crusts and radial branches. In this case, as with Tavernier mound, the framework was not current resistant and provided cores for rhodoliths. Shapes of the Miocene rhodoliths are similarly controlled by the nature of the framework, and the branching density by apical abrasion following transport. Thus crustose frameworks in the Miocene gave rise to discoidal rhodoliths whilst upright-branching frameworks on Tavernier mound give rise to ellipsoidal rhodoliths. Palaeocurrent directions in the Coralline Algal Biostrome are very varied and no separation of windward frameworks and leeward coralline algal gravels was detected.

Although coralline algae and algal limestones are common in the Tertiary, there are few detailed descriptions of the facies present. Therefore no further comparisons can be made at present but it is hoped that this study will help interpretation in the future.

Palaeoecological conclusions

This study provides further documentation of coralline algal facies occurring in windward reef environments. Although walled reef coralline facies are reasonably well known, coralline facies from carbonate mounds have not been previously studied in the Recent. The branching *Neogoniolithon* facies is a useful sea-level indicator as it occurs within a metre or so of low-water level. Perhaps of more use in palaeoecological studies is the growth response of this coralline alga to low-water level. Vertical growth is halted and a flat-topped framework is formed by sideways branch growth. This feature is also found in other shallow water coralline reefs and may well be applicable to other unrelated coralline algae in fossil sequences, thus giving a rare preservation of the former low-tide level. Conversely, the absence of a flat-topped framework cannot be used as an indicator of deeper water as domed frameworks may occur where there is greater tidal range, higher wave splash, or where sea-level changes are faster than coralline accretion.

The preservation potential of the *Neogoniolithon* framework is poor on Tavernier mound due to bioerosion of the algal thallus and later fragmentation by crustaceans. In ancient sequences the evidence for bioerosion and burrowing would be preserved, but careful study would have to be carried out to establish the existence of a former framework as opposed to unattached corallines (mearl; Bosence 1976). The small core samples from Tavernier mound did not recover many segments of framework but larger exposures may contain relics of the branching frameworks with unidirectional branch growth (cf. Bosence 1984), or alternatively these may be preserved in rhodolith cores. Portions of previous frameworks were found to be preserved in this fashion in the Miocene of Malta (Bosence and Pedley 1982).

The former existence of framework, rhodolith, and gravel-patch subfacies will again depend on preservation, which in turn relates to local sedimentation and burrowing rates. These subfacies are not recognizable in the Tavernier cores. If preserved elsewhere they may give an indication of lateral energy gradients within shallow water sequences.

Rhodoliths also contain considerable palaeoecological information which can be used not only in taxonomic comparisons with Holocene and Cainozoic examples but also with unrelated corallines. Rhodolith cores may give evidence of coralline algal facies which are not otherwise preserved. The numbers of redirected branch growths in the corallines give an indication of the amount of transport away from the framework facies and possibly the frequency of storms.

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Cover: The dinoflagellate cyst *Impagidinium patulum* (Wall) Stover and Evitt from bottom sediments in the North Atlantic Ocean. British Geological Survey specimen MPK 4234. ×2500.

PALAEOECOLOGY, TAPHONOMY, AND DATING OF PERMO-TRIASSIC REPTILES FROM ELGIN, NORTH-EAST SCOTLAND

by MICHAEL J. BENTON *and* ALICK D. WALKER

ABSTRACT. Three Permo-Triassic reptile faunas and one footprint fauna are known from the area of Elgin, north-east Scotland. The footprints are probably Permian in age and they indicate an assemblage of mammal-like reptiles. The mammal-like reptiles, pareiasaur and procolophonid from the Cutties Hillock Sandstone Formation (new name) are probably latest Permian in age. They were found at the base of an aeolian unit, just above pebbly sheet-flood deposits. The Lossiemouth Sandstone Formation is dated as Lower Norian on the basis of its varied reptile fauna. This fauna shows affinities with northern and southern hemisphere faunas of its time, and contains Britain's oldest dinosaur, the coelurosaur *Saltopus*. The Lossiemouth reptiles (*c.* 130 individual animals from four or more localities) were apparently preserved at the bases of barchan dunes and many of them just above flood plain deposits. Most of the skeletons are well preserved in articulation and only a few show disturbance, possibly by scavenging. The fauna consisted of *Hyperodapedon* and *Stagonolepis*, two moderate-sized herbivores (25% each), a selection of small omnivores: *Leptopleuron* (23%), *Brachyrhinodon* (9%), *Scleromochlus* (5%), and *Erpetosuchus* (2%), and a medium-large carnivore, *Ornithosuchus* (10%) and a small carnivore, *Saltopus* (1%). Some of the smaller animals show adaptations to living on sand. The last reptile fauna, from the Rhaetic of Linksfield, consists of odd bones of marine reptiles.

VERTEBRATE palaeontologists who study Mesozoic reptiles often concentrate on individual genera and do not record information on faunas. This paper presents information on the Elgin reptile faunas that we have gathered by personal observation of the specimens and the geology, and by studying unpublished documents and the scattered published literature.

Two main faunas of fossil reptiles are known from the neighbourhood of Elgin, north-east Scotland. The earlier, from the Cutties Hillock Sandstone Formation (defined below; probably latest Permian) consists of two genera of mammal-like reptiles, a pareiasaur and a procolophonid and the later, from the Lossiemouth Sandstone Formation (late Triassic) comprises at least four genera of thecodontians, a rhynchosaur, a sphenodontid, a procolophonid, and a coelurosaur dinosaur. A third fauna from the Rhaetic of Linksfield contains a few marine reptile bones. The Hopeman Sandstone Formation (in the restricted sense proposed in this paper, see below) has also yielded a fauna consisting of two or three kinds of footprints. Both main faunas are unusual in showing close affinities with those of southern continents as well as with those of the rest of western Europe and North America. Both faunas are also unusual in that the remains are preserved in aeolian deposits, clearly not the natural habitat of the majority of the animals.

The aims of this paper are fivefold: to review the composition of the faunas; to consider the sedimentology and environments of the reptile beds; to discuss the taphonomy of the remains; to assess the ecology of the late Triassic reptiles; and to review the relationships and age of the faunas. Most of the data have never been published before, and it is hoped that this paper will provide a useful summary of the Elgin reptiles and their environments. The taphonomic observations are original and should be of value for comparison with other aeolian deposits. Most attention will be devoted to the late Triassic fauna because of the larger number of remains, and its greater importance in Triassic faunal development.

Repository abbreviations used in this work are: BMNH, British Museum (Natural History); EM, Elgin Museum; GSE, Geological Survey Museum (Edinburgh); GSM, Geological Survey Museum (London); MM,

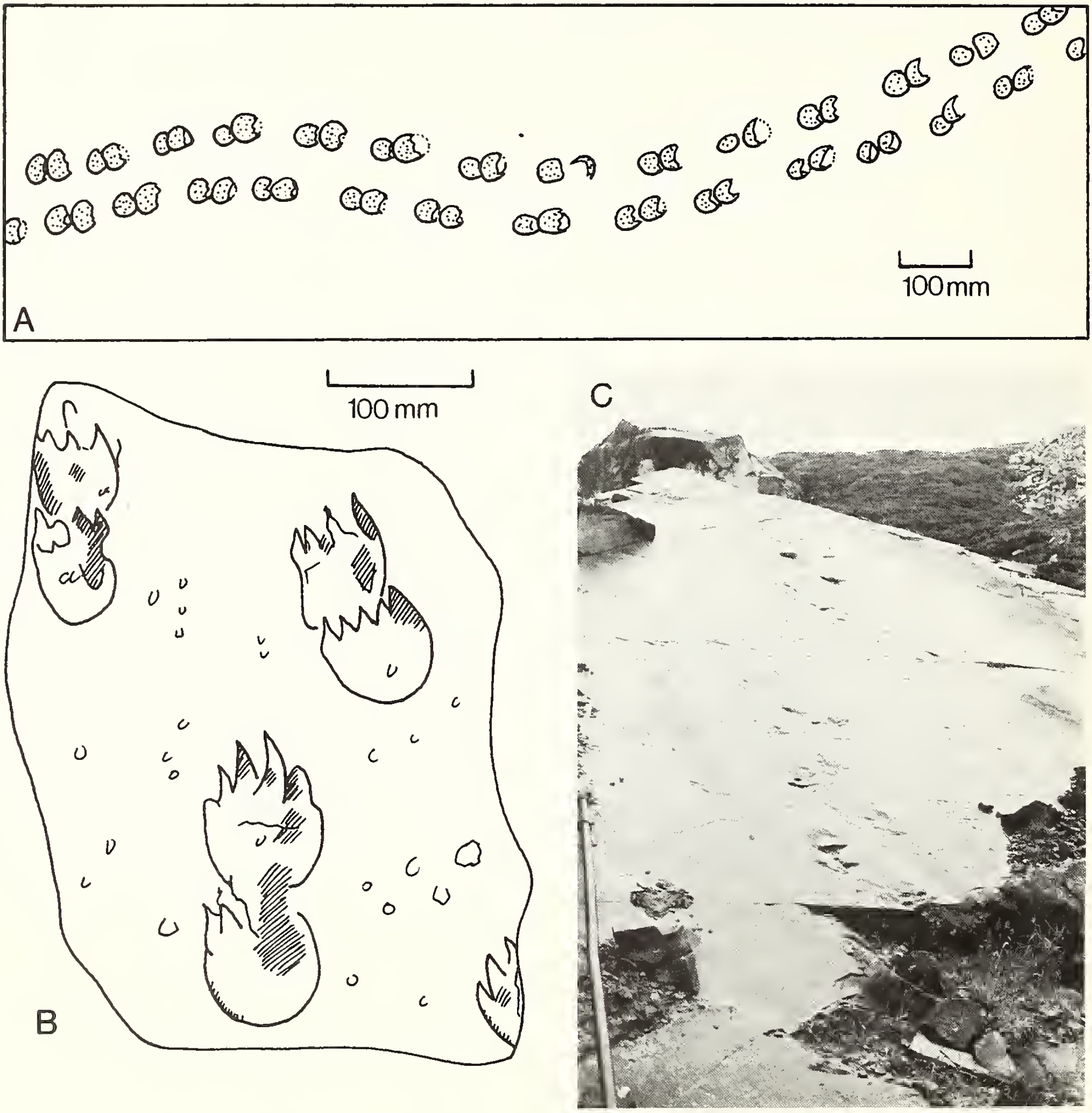
[Palaeontology, Vol. 28, Part 2, pp. 207–234.]

Manchester Museum; NUGD, Newcastle University, Geology Department; RSM, Royal Scottish Museum, Edinburgh.

THE FAUNAS

Footprints from the Hopeman Sandstone Formation

At least two kinds of footprint have been identified from the Hopeman Sandstone Formation. Type A (text-fig. 1A) (roughly circular, impressions 30–40 mm long, stride length 110–120 mm, width



TEXT-FIG. 1. Reptile footprints from the Hopeman Sandstone Formation, near Elgin (?late Permian). A, small prints, after Brickenden (1852); B, medium prints, *Chelichnus megacheirus*, after Huxley (1877, pl. 14); C, large prints, field photograph. A, B from Masonshaugh Quarry; C from Clashach Quarry. Scales are shown for A and B; C shows tracks which are 100–150 mm wide and have a stride length of 700–800 mm.

of trackway 80–90 mm, no sign of toe marks) is represented by a slab collected in 1850. This was the first fossil from Elgin recognized as reptilian, and the trackway was initially interpreted as having been formed by a tortoise (Brickenden 1850, 1852).

Numerous slabs of larger footprints (Type B, text-fig. 1B) were collected after that (Beckles 1859; Huxley 1859*b*; Hickling 1909). The fore- and hind-foot were clearly different. The print of the fore-foot is semicircular, about 40 mm long and 60 mm wide, with traces of four or five claws at the front. The print of the hind-foot is larger, about 90 mm long and 80 mm wide, with traces of five claws at the front. The prints overlap in pairs, and stride length was 300–400 mm. These were named *Chelichnus megacheirus* Huxley 1877. Larger specimens (print 170 mm long, 140 mm wide) were figured by Huxley (1877, pl. 15, fig. 6) and some similar tracks may still be seen on a large slab at Clashach Quarry (NJ 163702). These large tracks measure 150–250 mm long and 100–150 mm wide, and the stride length is 700–800 mm (text-fig. 1C). A possible third kind of track was described from the coast by Huxley (1877) and Hickling (1909, pl. 2, figs. 7, 8) and from Cutties Hillock (Watson and Hickling 1914). This is supposedly distinguished by having broader toes than Types A or B, but the generally smudged preservation of most specimens makes such a distinction inadvisable. The Hopeman footprints were probably formed by two or more mammal-like reptile genera, possibly dicynodonts (Haubold 1971).

Reptiles from the Cutties Hillock Sandstone Formation

Reptile bones were collected from a quarry on Cutties Hillock in 1884, and some nearly complete skeletons were obtained in 1884 and 1885 (Judd 1885, 1886a, b; Traquair 1886). Three genera were described by E. T. Newton (1893): *Gordonia*, *Geikia*, and *Elginia*.

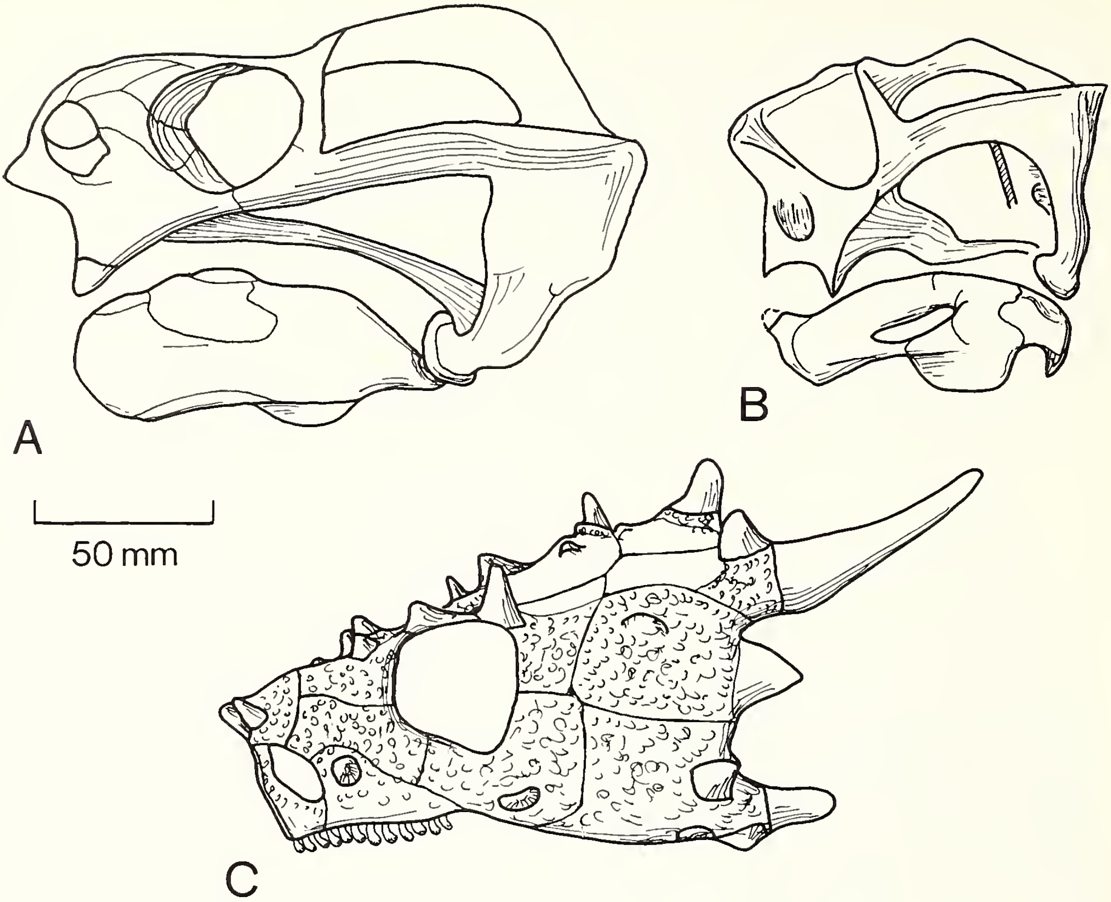
Gordonia and *Geikia* are dicynodonts, a group of herbivorous mammal-like reptiles most of which had no teeth except for a 'tusk'. *Gordonia* (text-fig. 2A) is represented by remains of the skulls and skeletons of eight to thirteen individuals, and four species were originally described, although they are perhaps all synonymous (Walker 1973). *Gordonia* had a heavy broad skull, 100–180 mm long, and it was clearly provided with powerful jaw muscles. The relationships of *Gordonia* are uncertain: Cluver and King (1983, p. 268) state 'possibly related to *Kingoria* or *Dicynodon*'. The single specimen of *Geikia* (text-fig. 2B) is unusual for its short, broad skull which was about 95 mm long (Newton 1893). *Geikia* has no teeth at all and the snout is box-like. Rowe (1980) has redescribed the specimen and assigned it to the family Cryptodontidae with a selection of late Permian dicynodonts from South Africa and Zambia. He also placed '*Dicynodon*' *locusticeps* from Tanzania in the genus *Geikia*, and noted that the closest relative of *Geikia* is *Pelanomodon*. Cluver and King (1983) placed *Pelanomodon* in the new Family Aulacephalodontidae, and Cruickshank and Keyser (1984) have confirmed this assignment of *Geikia*.

Elginia was a pareiasaur with a remarkably spinescent skull (text-fig. 2C). The 210 mm long holotype skull is broad and covered with rough pits and spines of various sizes. The teeth are leaf-like in shape, and *Elginia* was probably a herbivore. Other pareiasaur remains include vertebrae and a sacrum probably belonging to the holotype as well as an undescribed partial skeleton and skull.

A fourth reptile from Cutties Hillock is represented by a specimen that was described by Newton (1893, pp. 461–462, pl. 33, fig. 5) as a tail of ?*Gordonia*. This specimen consists of seven dorsal vertebrae, the blades of two scapulae and the blade of an ilium of a procolophonid (Walker 1973). Finally, remains of an un-named dicynodont were collected from nearby Knock of Alves (or York Tower) Quarry in 1953 by A.D.W.

Reptiles from the Lossiemouth Sandstone Formation (Table 1)

A slab containing scutes of the thecodontian reptile *Stagonolepis* (text-fig. 3A) was the first fossil found in the Elgin Permo-Triassic, but it was initially interpreted as a large ganoid fish (Agassiz 1844). Later finds of limb-bones led to its interpretation as a reptile (Huxley 1859*a*, *b*), and in particular as an ancestral crocodile (Huxley 1875, 1877). More recent study (Walker 1961) has shown



TEXT-FIG. 2. The reptiles of the Cutties Hillock Sandstone Formation of Cutties Hillock Quarry, near Elgin (?latest Permian–early Triassic). Skulls of A, *Gordonia*; B, *Geikia*; and C, *Elginia*, all drawn to the same scale. (A, after Newton 1893; B, after Newton 1893 and Rowe 1980; C, after Newton 1893 and original.)

that it was an aetosaur—a probable herbivore. *Stagonolepis* is represented by skull and skeletal remains of thirty or more individuals which were up to 2·7 m long. The snout had a curious blunt end, probably for digging, and the teeth were peg-like. *Stagonolepis* was shaped rather like a crocodile and had an extensive armour around its body.

The first Elgin reptile to be recognized as such was *Leptopleuron lacertinum* Owen 1851 (objective synonym, *Telerpeton elginense* Mantell 1852), based on a small skeleton collected at Spynie (Benton 1983*c*). Further finds (Huxley 1867; Boulenger 1904; Huene 1912a, 1920) showed it to be a procolophonid, a small omnivorous or herbivorous reptile with a triangular, spiked skull (text-fig. 3E). The skull was about 52 mm long, and the body may have been up to 400 mm in total length.

The third animal to be obtained from the Lossiemouth Sandstone Formation was named *Hyperodapedon* by Huxley (1859a). It was interpreted as a rhynchosaur (Huxley 1869, 1887; Burckhardt 1900; Boulenger 1903; Huene 1929; Benton 1983*d*, 1984), a group of diapsid reptiles that were abundant in many faunas worldwide in the middle and late Triassic. Its closest relative is *H. huxleyi* from the Maleri Formation of India. *Hyperodapedon* was a bulky 1·3 m long quadruped

TABLE 1. Classification of the reptiles of the Lossiemouth Sandstone Formation.

SUBCLASS ANAPSIDA
- Family Procolophonidae Cope 1889
  - *Leptopleuron lacertinum* Owen 1851 (objective junior synonym, *Telerpeton elginense* Mantell 1852)

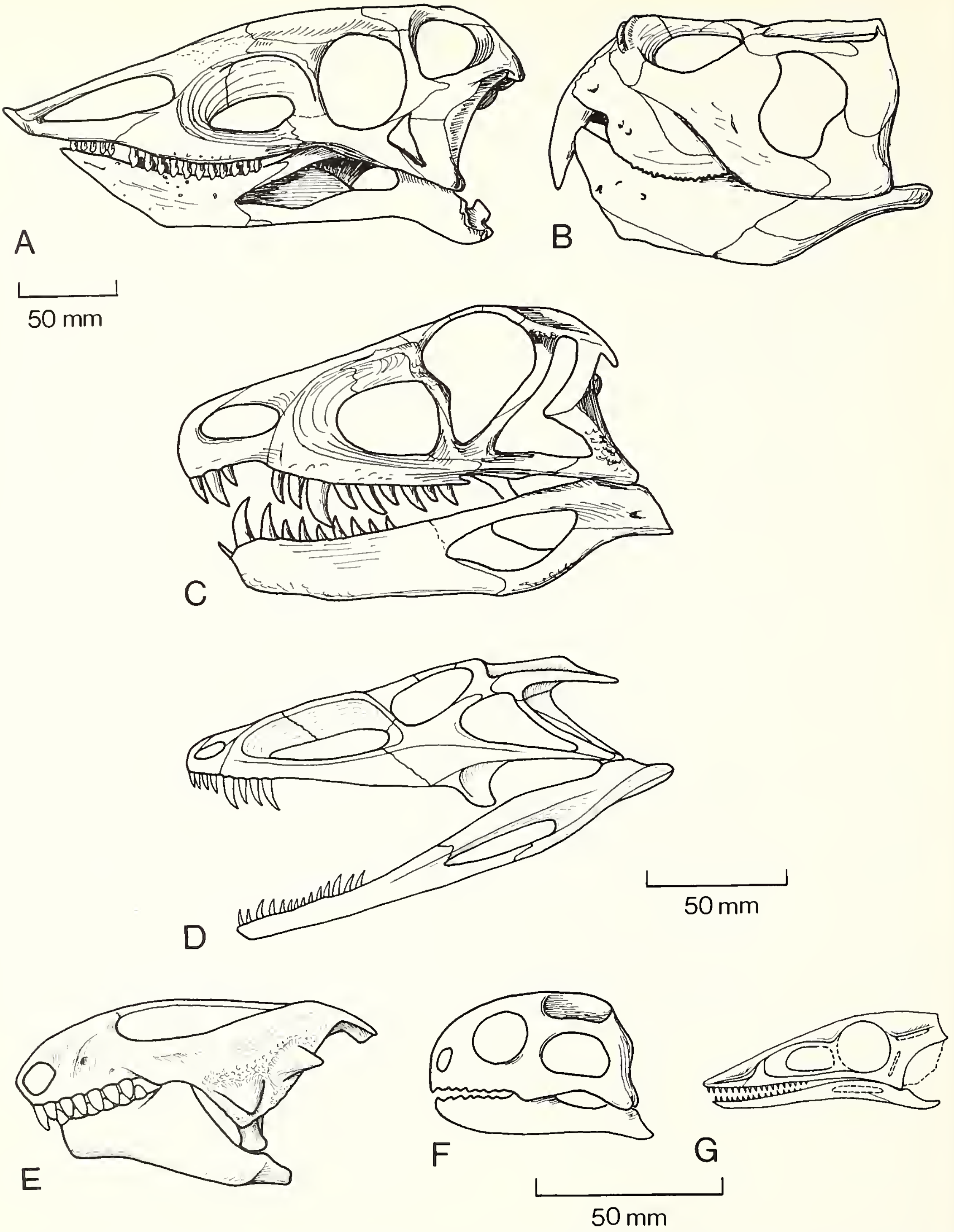
SUBCLASS DIAPSIDA
- Cohort Archosauromorpha Huene 1946
  - Superorder Rhynchosauria Osborn 1903
    - Family Rhynchosauridae Huxley 1887
      - *Hyperodapedon gordoni* Huxley 1859 (subjective junior synonym, *Stenometopon taylori* Boulenger 1903)
  - Superorder Archosauria Cope 1869
    - Order Thecodontia Owen 1859
      - Family Stagonolepididae Lydekker 1887
        - *Stagonolepis robertsoni* Agassiz 1844
      - Family Ornithosuchidae Huene 1908
        - *Ornithosuchus longidens* (Huxley 1877) (subjective synonyms, *Dasygnathus longidens* Huxley 1877; *O. woodwardi* Newton 1894; *O. taylori* Broom 1913)
      - Family Erpetosuchidae Watson 1917
        - *Erpetosuchus granti* Newton 1894
      - Family Scleromochliidae Huene 1914
        - *Scleromochlus taylori* Woodward 1907
    - Order Saurischia Seeley 1888
      - Family Procompsognathidae Huene 1921
        - *Saltopus elginensis* Huene 1910
- Cohort Lepidosauromorpha Benton 1983
  - Superorder Lepidosauria Haeckel 1866
    - Order Sphenodontia Williston 1925
      - Family Sphenodontidae Cope 1870(?)
        - *Brachyrhinodon taylori* Huene 1910

with strong limbs—the hind-foot had large claws and was probably adapted for scratch digging. The skull was the most remarkable feature (text-fig. 3B). It was 100–200 mm long and very broad at the back—there was an anterior premaxillary 'beak' and the teeth were arranged in multiple rows on the maxilla. The dentary had a sharp edge and it cut into a groove in the maxillary toothplate, providing a strong shearing bite.

Remains of the medium-sized carnivore *Ornithosuchus* (text-fig. 3C) were described by Huxley (1877), Newton (1894), Boulenger (1903), Broom (1913), Huene (1914), and Walker (1964). This animal was probably partly quadrupedal and partly bipedal, and it had sharp dagger-like teeth. Several specimens are known and these indicate a range in skull length of 50 to 450 mm and in body length of 0·5–3·5 m. *Ornithosuchus* was regarded by Walker (1964) as an ancestral carnosaur, but comparison with *Riojasuchus* (Bonaparte 1969) suggests that it had a 'crocodile-reversed' type of ankle joint (Cruickshank 1979) rather than the mesotarsal joint typical of dinosaurs, and was thus a thecodontian closely related to some South American forms (Bonaparte 1969).

A second small carnivore (or insectivore) is *Erpetosuchus* which was collected from a block built into a wall in Lossiemouth in the early 1890's (Newton 1894). The specimen includes a skull (text-fig. 3D), the fore-limbs and shoulder girdle, and the armour plates, which indicate a total body length of about 600 mm. It seemed to have some crocodilian characters (Walker 1968), but these were later considered to be the result of convergence. *Erpetosuchus* is another advanced pseudosuchian thecodont with a narrow 75 mm long skull which has a huge antorbital fenestra and a broad 'square' posterior skull roof (Walker 1970, pp. 364, 367–368; Krebs 1976, pp. 87–89).

Extensive collecting by William Taylor, a local naturalist, between 1890 and 1920, produced abundant remains of these animals from Lossiemouth and Spynie, as well as the holotypes of three new genera: *Scleromochlus*, *Saltopus*, and *Brachyrhinodon*.



TEXT-FIG. 3. The reptiles of the Lossiemouth Sandstone Formation, near Elgin (late Triassic: early Norian). Skulls of A, *Stagonolepis*; B, *Hyperodapedon*; C, *Ornithosuchus*; D, *Erpetosuchus*; E, *Leptopleuron*; F, *Brachyrhinodon*; and G, *Scleromochlus*, drawn to three different scales (A–C, D, E–G). The skull of *Saltopus* is not known. (A, after Walker 1961; B, after Benton 1983*d*; C, after Walker 1964; D, original; E, original; F, after Huene 1910*b*; G, original.)

Scleromochlus was based on several skeletons which showed an animal with a short body, short forelimbs, but long hindlimbs and long tail (Woodward 1907; Huene 1914). The skull (text-fig. 3G) is relatively large, but very lightly built. Overall body length was about 250 mm. *Scleromochlus* is a fourth thecodontian whose skull specializations suggest a relationship to the aetosaurs (Walker 1970, p. 361; Krebs 1976, p. 90). One specimen (BMNH R3146) shows transverse bands of thin dorsal scutes, figured by Woodward (1907) as abdominal ribs.

Saltopus (text-fig. 6A), represented by only one skeleton, and unfortunately lacking the skull, is Elgin's only dinosaur (Huene 1910*a*). The vertebrae and limbs are rather poorly preserved in outline, and the total body length was probably about 600 mm. It is a coelurosaur (Walker 1970, p. 359), and may be a podokesaurid (Huene 1914; Steel 1970) or a 'procompsognathid' (Romer 1966).

Brachyrhinodon (text-fig. 3F; Huene 1910*b*, 1912*b*) was a small animal 200–250 mm long, with a short snout, acrodont teeth, and teeth on the palate. It was probably an omnivorous sphenodontid related to *Polysphenodon* from the late Triassic of Germany (Walker 1966).

One small undescribed thecodontian is represented by a 'somewhat obscure skeleton in Manchester Museum' (MM L8270; Watson 1909*a*). This consists of a disarticulated skull, some of the skeleton, and some scutes. It is probably a new form, but is too poor to be described.

The record of a lungfish tooth-plate from Spynie, identified as *Ceratodus* (Traquair 1895, p. 280) is an error. This record is attributed by Taylor (1920) to Huxley, but he gives no reference and we have been unable to find that Huxley mentions it. The earliest reference appears to be that of Judd (1886a). The error was caused by confusion between the Triassic locality 'Spynie' and 'New Spynie' (now called Quarrywood), which lies on Upper Old Red Sandstone 4 km to the west. This was pointed out by Taylor (1920) and has been confirmed by one of us (A.D.W.) from examination of the matrix of the original specimen (EM 1978.348.1A, B) and from the making of casts from it. The tooth-plate is probably of *Phaneropleuron* (T. S. Westoll, pers. comm.) and the locality is most likely Leggat Quarry (NJ 176635), 850 m to the south-west of Quarrywood, as suggested by Taylor (1901, p. 48).

Reptiles from the Rhaetic of Linksfield

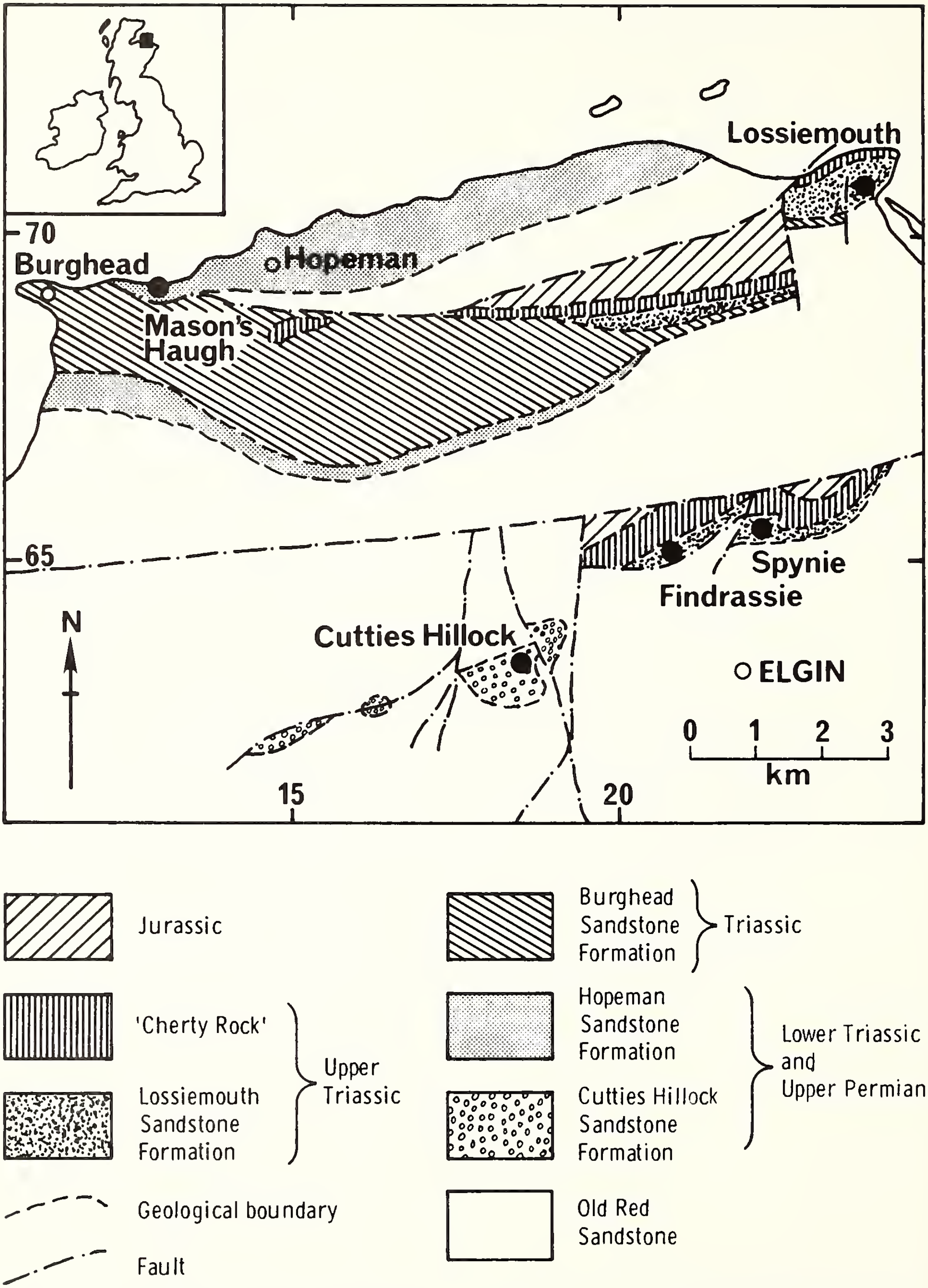
A large glacial erratic at Linksfield, near Elgin (NJ 222641) has yielded some reptile remains, as well as fish. The sediments were originally determined as Purbeck or Wealden (Duff 1842), but they were later dated as Rhaetic (Moore 1860, Jones 1863, Anderson 1964) on the basis of the fish and ostracods. Duff (1842, pl. 4.5) figured spines, scales, and teeth of such fish as *Hybodus*, *Lepidotes*, *Sphenonchus*, and *Acrodus*, as well as a plesiosaur vertebra and teeth, and a femur of a 'chelonian reptile' which Seeley (1891) later described as the femur of a crocodile *Saurodesmus robertsoni*.

STRATIGRAPHICAL TERMINOLOGY

The Permo-Triassic of the Elgin area outcrops in two belts, one along the coast between Burghead and Lossiemouth, and the other in the region of Elgin itself (text-fig. 4). The beds near Elgin occur in small fault-blocks within petrologically similar Upper Old Red Sandstone.

The nomenclature of the Hopeman and Cutties Hillock sandstones

Formal lithostratigraphical terms for the main units of the Permo-Triassic of the Elgin area were introduced by Warrington *et al.* (1980). The Hopeman Sandstone Formation was proposed to include predominantly aeolian sandstones some 60 m thick cropping out along the coast between Cummingstown and Covesea Skerries Lighthouse, and also for a separate strip of similar rocks, 30–45 m thick, lying on top of the Quarry Wood ridge and in the Knock of Alves area to the west of Elgin. Although there is some evidence which suggests that the sandstones of these two regions are broadly equivalent, and while it is true that the coastal sandstones are much better exposed (although the base is not seen), the combination of these two units is not altogether logical and has other undesirable consequences. The most important of these is that the name 'Cutties Hillock' for a world-famous fossil vertebrate locality and set of beds has disappeared, to be replaced by an unfamiliar


70
Burghead
Hopeman
Lossiemouth
Mason's Haugh
65
N
Cutties Hillock
Spynie
Findrassie
ELGIN
0 1 2 3
km
15
20
Jurassic
Burghead Sandstone Formation
Triassic
'Cherty Rock'
Lossiemouth Sandstone Formation
Upper Triassic
Hopeman Sandstone Formation
Cutties Hillock Sandstone Formation
Lower Triassic and Upper Permian
Geological boundary
Fault
Old Red Sandstone

TEXT-FIG. 4. The distribution of the Permo-Triassic beds around Elgin, north-east Scotland. The formations are indicated by shading, and the main reptile and footprint localities are named.

name. Furthermore, apart from a small scrap of bone (Peacock *et al.* 1968, p. 59) the coastal sandstones have yielded nothing but reptilian tracks, whereas the reptilian fauna comes entirely from the inland localities. Thus the accurate determination of the age of this Formation has to be obtained from a study of the reptiles, none of which occurs in the type area.

The tracks from the coastal sandstones are believed to have been made by dicynodont reptiles, but this is a group which ranges in time from the middle of the Permian until late in the Triassic. Hickling (1909) considered that the closest comparisons of these tracks were to be made with those from Mansfield and Penrith. According to Smith *et al.* (1974), the Mansfield Stone is a variety of the Lower Magnesian Limestone and is thus early Upper Permian in age, while the tracks from Penrith are late Lower Permian. In contrast, the Cutties Hillock fauna is probably very late Permian in age (see below). Tracks were also seen at Cutties Hillock Quarry itself in 1878 before the reptiles were discovered (Peacock *et al.* 1968, p. 73) and have occasionally been seen since. A single small print from a nearby quarry, the position of which is now uncertain, was figured by Watson and Hickling in 1914. However, these tracks can surely only be used as evidence of a broad time-equivalence between the sandstones of the two areas.

Glennie and Buller (1983) have suggested that the Hopeman Sandstone on the coast could be divided into two units, a lower one of late Lower Permian age, and an upper one, presumed to be equivalent to the Cutties Hillock beds and thus of latest Permian age. They considered that the contorted sandstones seen in the coastal sections lie at the same stratigraphical horizon and owe their origin to the Zechstein marine transgression. Williams (1973), on the other hand, divided the coastal sandstones into four successive phases, the first three of which terminated in contorted strata (he followed Peacock *et al.* (1968), however, in regarding the coastal and inland strips as time-equivalents).

While we do not agree with the conclusions of Glennie and Buller (1983) concerning the subdivision of the Hopeman Sandstone on the coast, these differences of interpretation serve to underline the necessity for a separate formal lithostratigraphical unit to include the reptile-bearing beds, to avoid confusion, and until such time as definite correlations shall have been established. It is proposed, therefore, that these inland beds be termed the *Cutties Hillock Sandstone Formation*.

Peacock *et al.* (1968) preferred to use the name 'Sandstones of Cutties Hillock (Quarry Wood)' instead of 'Cutties Hillock Sandstone' because 'Cutties Hillock' does not occur on Ordnance Survey maps (it does actually appear on a map by Gordon (1892)). However, this is not a strong objection, since the position of the quarry is given by Judd (1886*a*, pp. 397–398) and is well established by local tradition. The term 'Cutties Hillock Sandstone Formation' has in fact already been used by Smith *et al.* (1974, p. 25), although not formally defined.

Origin and correct form of the name Cutties Hillock

Although various suggestions have been made, including 'short hillock' and 'witches' hillock', it seems most likely that the name derives from a Gaelic original. It does not seem to have appeared in print until after the discovery of the reptiles in 1884. Mackie, an important worker on the local geology and discoverer of the Rhynie Chert, always used the form 'Cuttieshillock' in several papers (e.g. 1897) and in articles in local newspapers. Other local writers tended to do the same; furthermore, the old labels on the specimens from this locality in Elgin Museum also use this form. Maxwell (1894) mentions, among other similar names, 'Kittyshalloch' in Galloway and 'Cuttyshallow' in Ayrshire. In the last instance he gives the derivation as the Gaelic *ceide sealghe*, pronounced to sound something like 'keddyshalluh' and meaning 'hill-brow of the hunting'. It appears, therefore, that originally the name had nothing to do with the words 'cutty' or 'hillock', but when it was written down, authors tended to split it into two words, transferring the 's' to the first of these and sometimes adding a singular or plural apostrophe as seemed appropriate.

However, in the interests of stability of nomenclature and since writers on the derivation of place-names often disagree strongly with each other, it seems better to rely on first published usage in the scientific literature. This is that of Judd (1885, p. 573), who speaks of the 'Cutties Hillock quarry', and this usage, omitting the apostrophe, is by far the most common in the literature.

Cutties Hillock Sandstone Formation

Type area. Quarries and natural exposures on Quarry Wood ridge, the Knock of Alves and Carden Hill west of Elgin. The formation is seen to rest unconformably on Rosebrae Beds of the Upper Old Red Sandstone in Rosebrae Quarry (NJ 173633) and York Tower Quarry (NJ 162629). The reptile fauna comes mainly from Cutties Hillock Quarry (NJ 185638).

The classification of the Elgin Permo-Triassic

The classification of the Permo-Triassic rocks around Elgin, using the new terminology (Warrington *et al.* 1980), and as recommended here, is:

Cherty Rock (?Norian–Rhaetian)

Lossiemouth Sandstone Formation (Carnian–Norian)

(Synonyms: Reptiliferous Sandstone (pars) (Symonds 1860; Harkness 1864; Judd 1873, 1886*a*, *b*; Gordon 1892; Traquair 1895; Mackie 1897; Boulenger 1903); Elgin Sandstone (Newton 1894); *Stagonolepis* Beds (Boulenger 1904; Huene 1910*a*); *Stagonolepis* Sandstone (Watson 1909*b*; Huene 1910*b*, 1912*a*, *b*, 1913, 1914); Sandstones of Lossiemouth, Spynie, and Findrassie (Westoll 1951); Sandstones of Spynie, Lossiemouth, and Findrassie (Peacock *et al.* 1968)).

Burghead Sandstone Formation (??Anisian–Carnian)

(Synonyms: Burghead Sandstones (Westoll 1951); Burghead Beds (Peacock *et al.* 1968)).

Hopeman Sandstone Formation (Late Permian)

(Synonyms: Sandstones of Cummingstone (Huxley 1859*b*, 1877); Cummingstone Beds (Hickling 1909; Watson 1909b; Watson and Hickling 1914); Reptiliferous Sandstone (pars) (Symonds 1860; Harkness 1864; Judd 1873, 1886*a*, *b*; Traquair 1895); Sandstones of Cutties Hillock and Hopeman–Cummingstone (pars) (Westoll 1951); Sandstones of Cuttie Hillock (Quarry Wood) and Hopeman (pars) (Peacock *et al.* 1968)).

Cutties Hillock Sandstone Formation (Late Permian)

Reptiliferous Sandstone (pars) (Judd 1886*a*, *b*; Traquair 1895; Mackie 1897); Elgin Sandstone (Gordon 1892; Newton 1893); Cutties Hillock Beds (Watson 1909*b*; *Gordonia* Beds (Boulenger 1904); *Gordonia* Sandstone (Huene 1913); Sandstones of Cutties Hillock and Hopeman–Cummingstown (pars) (Westoll 1951); Sandstones of Cutties Hillock (Quarry Wood) and Hopeman (pars) (Peacock *et al.* 1968); Cuttie's Hillock Sandstone (Walker 1973)).

OCCURRENCE OF THE REPTILES

Sedimentology of the Hopeman Sandstone Formation (s.s.)

The Hopeman Sandstone Formation of the coast between Cummingstown and Covesea Skerries and Halliman Skerries, some 60 m thick, shows evidence of largely aeolian deposition: large-scale cross-bedding is common, and the sandstones are generally composed of well-rounded grains of quartz and felspar, often of high sphericity, with only a little mica (Peacock *et al.* 1968, p. 59). However, the action of water is indicated in places by lenses of coarse sandstone and well-rounded pebbles with small-scale cross-bedding, as well as contorted beds (Peacock 1966). Williams (1973) identified four phases of dunes: seif dunes at the base, followed by three phases of barchan dunes. Each of the first three phases is topped by contorted beds and sheet flood or playa lake deposits. The fossil tracks have been obtained principally from Masonshaugh Quarry, Cummingstown (NJ 125692). Occasional footprints have been observed in Greenbrae Quarry (NJ 137692) and Clashach Quarry (NJ 163702), and Peacock *et al.* (1968, p. 59) report an unidentifiable bone fragment from Greenbrae.

Taphonomy of the Hopeman Sandstone Formation footprints

The footprints of the Hopeman Sandstone Formation may be preserved on low-angle dune foresets, but this has only been observed in a few *in situ* occurrences. The slabs collected in the nineteenth century may include some from horizontal bedding planes. However, there is usually a mound of sand behind each print (Brickenden 1852; Huene 1913; Watson and Hickling 1914), and this would suggest that the animals were moving uphill. These mounds are seen also behind the large footprints at Clashach (text-fig. 1C).

Martin (*c.* 1860) gave a detailed account of the occurrence of tracks at Masonshaugh, and notes that they were all heading in one direction (towards today's North Pole). He considered that the producers were moving down to the Moray Firth across the beach to feed in the sea! The Elgin footprints may be interpreted as individual trackways formed by two or three species of mammal-like reptiles, each displaying a range of sizes, heading across a dune-field towards the centre of the depositional basin to the north.

Sedimentology of the Cutties Hillock Sandstone Formation

The Cutties Hillock Sandstone Formation is between 30 and 45 m thick. It may be divided into two units (Peacock *et al.* 1968; Williams 1973): a lower phase (up to 4 m thick) consisting of a series of pebbly sandstones that lie discordantly on the Old Red Sandstone, and an upper phase which consists of about 30 m of large-scale light brown and yellow cross-bedded sandstone. The lower pebbly beds have been interpreted as sheet flood deposits, but the presence of dreikanter pebbles with rounded edges suggests that they were exposed to wind erosion before being reworked by water (Mackie 1902; Watson 1909*b*; Watson and Hickling 1914; Williams 1973). The upper phase shows well-rounded quartz grains and unidirectional foresets which indicate fossil barchan dunes. The reptiles *Elginia*, *Gordonia*, and *Geikia* came from Cutties Hillock Millstone Quarry (NJ 185638) and an isolated footprint and other trackways were found nearby (Linn 1886; Huene 1913; Watson and Hickling 1914), Walker (1973) found an un-named dicynodont in York Tower Quarry, Knock of Alves (NJ 162629). An unidentified bone in Forres Museum was found in Crownhead Quarry (NJ 183630) on the south side of Quarry Wood hill and is of interest as the only bone recorded from this part of the outcrop. A slab in Elgin Museum showing footprints with a tail-drag on top of ripple-marks probably came from 'Robbies Quarry', the position of which is uncertain, but it was probably one of the Crownhead group of quarries.

Taphonomy of the Cutties Hillock Sandstone Formation reptiles

The reptiles from the Cutties Hillock Sandstone Formation appear to have been collected from the base of the upper phase, just above the pebbly sandstones. Judd (1886*a*, pp. 400–401) noted that 20 feet (6·2 m) of the 'Reptiliferous Sandstone' was to be seen above the pebbly layers, and that the remains of five reptiles all came from one horizon and that a sixth came from the bed below. Phillips (1886) confirmed this. Gordon (1892, p. 242) referred to 'a portion of this conglomerate containing reptilian remains'. Newton (1893, pp. 462, 466) also noted that the specimens of *Gordonia juddiana* and *Geikia elginensis* contained pebbles in the matrix like those of the 'conglomerate' bed. There are also pebbles in the specimen of *Gordonia duffiana*. These blocks (EM 1978.559.1, 2) show quartz pebbles up to 20 mm and up to 7 mm in diameter respectively.

The skeletons are well articulated, and some show series of vertebrae, ribs, and limbs with the skull in position. The type of *Elginia* (GSE 4783–4788) lacks its lower jaws. Details of the association of parts have been lost in some specimens, however, because only parts were collected and sufficient care was not exercised in keeping associated blocks together. The animals are preserved generally on their sides, although one pelvis (RSM 1966.42.3) is spread out flat. *G. duffiana* (EM 1978.559.1, 2), however, has the vertebrae and some limb bones passing vertically into the plane of bedding. In general, the 'long' skulls appear to be preserved on their sides, and the 'wide' skulls lie flat with the skull roof parallel to the plane of bedding, or in a vertical 'nose down' attitude (e.g. RSM 1956.8.3).

Individual bones may be distorted. The bones are represented by cavities in the rock from which virtually all bone material has disappeared, and the interface with the sandstone may be stained with black material containing iron, manganese, and cobalt (Newton 1893, p. 435). The cavities may be compressed with opposite impressions almost touching. Limb bones may be particularly flattened, and the ends may be hard to interpret either because of poor preservation and compression, or because the ends were largely cartilaginous in life. The centra of the dicynodont vertebrae are usually missing or very poorly preserved, although neural arches and ribs may be easy to cast. By contrast, the centra of *Elginia* are well preserved. Skulls are often vertically compressed (Newton 1893; Walker 1973; Rowe 1980), and in *G. duffiana* most of the squamosals and the right half of the occiput are missing, which presumably indicates post-mortem, pre-fossilization damage.

Sedimentology of the Lossiemouth Sandstone Formation

The Lossiemouth Sandstone Formation is distributed in several small fault-bounded blocks at Lossiemouth, Spynie, and Findrassie (Peacock *et al.* 1968, pp. 67–69; Williams 1973). The thickness of the unit varies from 7 to 30 m. It is underlain by strata which have been interpreted as a thin representative of the Burghead Sandstone Formation. Peacock *et al.* (1968) suggested that the Burghead Sandstones (mainly point bars in their type area, according to Williams (1973)) interdigitate with the Lossiemouth Sandstones to the west and, following Westoll (*in* Watson *et al.* 1948), they interpreted the thin calcareous sandstones below the typical Lossiemouth Sandstone Formation at Lossiemouth as a reduced lateral equivalent of the Burghead Sandstone Formation. However, this interpretation is hard to prove because there is a large geographic gap between the outcrops of typical Burghead and typical Lossiemouth beds, and because we have no information on what succeeds the Burghead Sandstones in their type area. The Lossiemouth Sandstone Formation is overlain by the Cherty Rock (sandy limestone and chert).

The Lossiemouth Sandstones are white, buff, yellow, or pinkish. Grain size is usually uniform (0·2–0·5 mm) with grains well-rounded. The rock is composed of quartz, feldspar, and rare brownish chert and quartzite. Cements are usually overgrowths of secondary quartz and feldspar, but calcite and fluorspar may also occur (Peacock *et al.* 1968, pp. 69–70).

The sandstones may be finely laminated, but more usually they show large-scale cross-beds on well-weathered surfaces. These features, as well as the absence of pebbles, the rarity of micas and heavy minerals, strongly suggest aeolian deposition.

Foreset analysis of the cross-beds indicates a prevailing south westerly wind forming barchan dunes. These have been interpreted (Williams 1973, pp. 132–135) as reworked sand from the underlying Burghead Sandstone Formation, which he regards as composed of flood-plain sandstones at Lossiemouth. Dunes up to 20 m high migrated across the flood plain during arid periods, and the aeolian deposition was terminated by large-scale flooding and the deposition of silicified and calcareous sandstone ('Sago Pudding Sandstone', Peacock *et al.* 1968, p. 71; Williams 1973, pp. 136–143: upper part of Lossiemouth Sandstone Formation).

The reptiles were obtained from Lossiemouth East Quarry (NJ 236707), Lossiemouth West Quarry (NJ 231704), Spynie (NJ 223657, and others), and Findrassie (NJ 202650?). Taylor (1920) reported a specimen of *Leptopleuron* (EM 1920.5) from a glacial erratic of Triassic beds on the Hill of Meft, north-west of Urquhart (NJ 268642).

Taphonomy of the Lossiemouth Sandstone Formation reptiles

The skeletons of *Stagonolepis* and *Hyperodapedon* were apparently found just above the base of the Lossiemouth Sandstone Formation. Murchison (1859, p. 428) stated that the bones found then were collected 'in the lowest part' of the freestones being quarried at Lossiemouth. Gordon (1859, p. 46) confirmed this, stating that the lowest beds at Lossiemouth were red clay, succeeded by yellowish soft sandstone and then harder sandstone. The red clay may be equivalent to that reported by Peacock *et al.* (1968, p. 65) as 'micaceous siltstone', the yellowish soft sandstone may be the 'Burghead Beds equivalent', and the harder sandstone is probably the Lossiemouth Sandstone Formation. The bones were found 'immediately under this hard siliceous sandstone in a quarry half-way to the new harbour from Rockhouse, and in the face of the wall of rock that overhangs the houses fronting the old harbour . . .'. This refers to the east end of Lossiemouth East Quarry (NJ 237707). Judd (1873, p. 137) stated that the reptiles were found '100 ft. below the top of the sandstones', which would imply about the base of the Lossiemouth Sandstone Formation, if its complete thickness is taken into account. Judd (1886*a*, pp. 397, 403) added that the reptile remains all came from 'a single band of soft rock'. Further, Gordon (1892, p. 245) suggested that 'if any excavation were to be made for fossils alone, it should be, in the first place, in the Lossiemouth quarries, and in the platform left by the quarrymen.

They did not go further down, because the bed was softish and rubbly, but it was at this horizon more than elsewhere in the quarry that most fossils were found.'

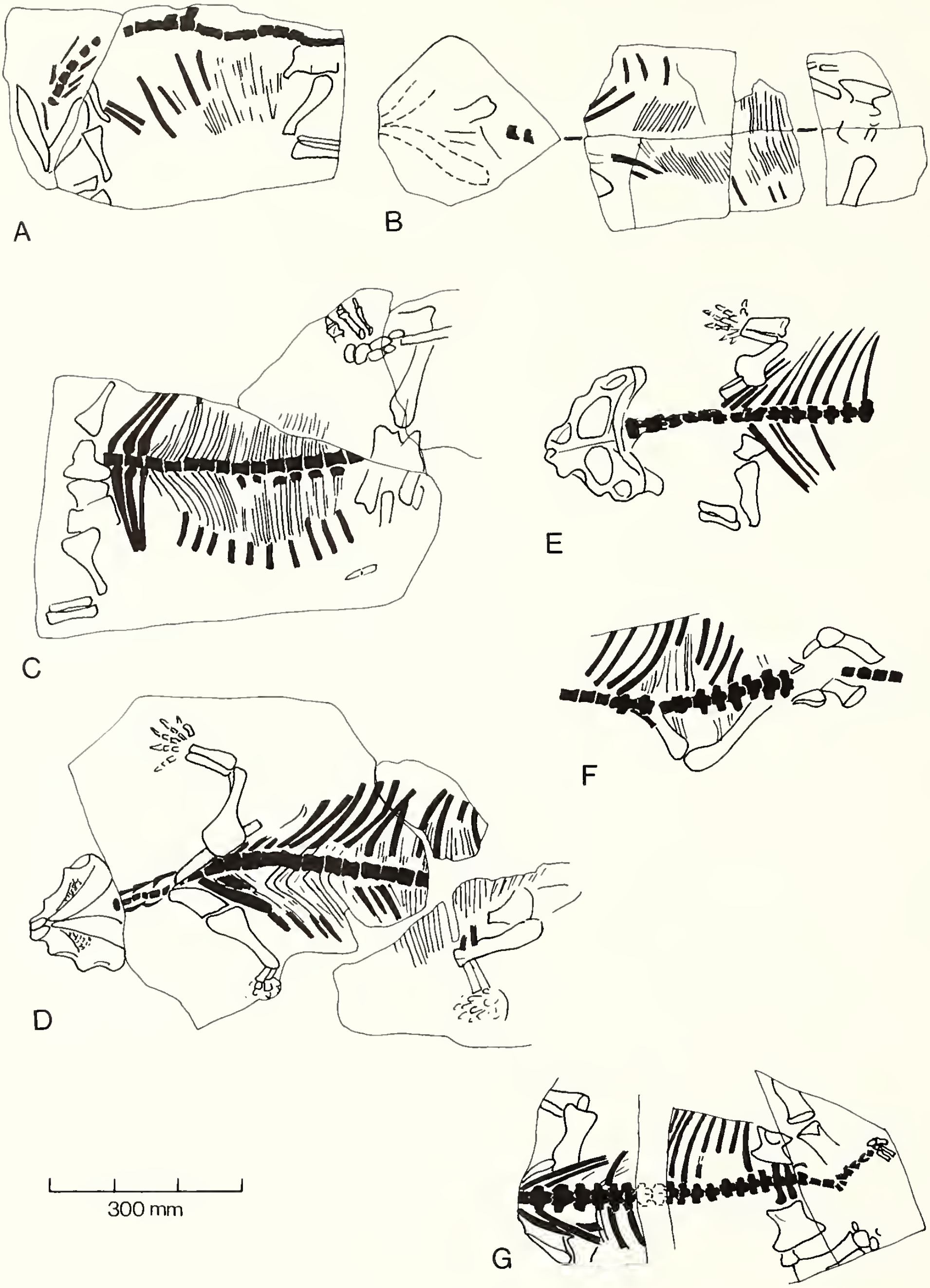
At Spynie the reptiles also appear to have been found low in the Lossiemouth Sandstone Formation. The type specimen of *L. lacertinum* 'was found by Mr. William Young at the bottom of a shaft which had been sunk through 51 feet of sandstone down to a soft rubbly bed' (Duff *in* Murchison 1859, p. 435). Gordon (1859, pp. 45–46) added that the specimen was 'extracted from the living rock, deep in a quarry opened on the west end of the hill' and Martin (*c*. 1860) stated that the specimen was 'found low down, in the bottom of the quarry'. The quarry has been identified as an old pit at NJ 2206 6557 (Peacock *et al.* 1968, p. 68). *Hyperodapedon* apparently came from another pit nearby: 'the most westerly of the Spynie quarries' (NJ 2192 6555) (Gordon *in* Huxley 1877; Linn 1886; Peacock *et al.* 1968, p. 68). These openings were probably abandoned over 100 years ago, judging by the large trees growing in them, and *Ornithosuchus*, collected in 1891, may have come from the large quarry still in operation (NJ 2225 6565). This was the site of two fine skulls of *Hyperodapedon* collected in about 1948 (now in RSM).

The first finds of *Stagonolepis* from Findrassie were made 'near the east entrance to Findrassie House, and among the debris of a pit opened up for road material' (Gordon 1859, p. 44). The East Lodge of the Findrassie Estate is situated at NJ 2074 6545, and the pit could be one of the remaining Findrassie quarries which lie south and south-west of the entrance (Peacock *et al.* 1968, p. 69), or it could have been filled (Walker 1961, p. 106). On the original geological survey of the Elgin area, Linn (1886) recorded that *Stagonolepis* was found 'in the more westerly' of a line of three quarries (?NJ 2015 6495). Peacock *et al.* (1968, p. 137) suggest a more easterly pit at NJ 205651 as the source of the reptiles. Most of the Findrassie specimens figured by Huxley (1877) are in the form of well-preserved moulds. However, some specimens in Elgin Museum labelled 'Findrassie' look different and have bone preserved—this may indicate a different locality. There are occasional pebbles in the matrix, and the early specimens at least occurred at the base of the reptiliferous sandstone, just above the Upper Old Red Sandstone (Gordon 1859; Walker 1961).

Unfortunately, in no case is it clear what relationship the skeletons bore to the ancient dunes. Some of the *Stagonolepis* slabs from Lossiemouth in the RSM show cross-bedding and slightly more mica than usual on the base. The aeolian foreset cross-bedding is generally only visible in the lower parts of the Lossiemouth Sandstone Formation, because of extensive silicification higher up (Williams 1973). This again confirms the suggestion that most of the reptile specimens came from near the base of the formation. There is very little mica in typical Lossiemouth Sandstones, but there is up to 6% of total composition in the underlying flood plain deposits, and small amounts also in the overlying Sago Pudding Sandstone.

Outline sketches of the more complete skeletons of *Hyperodapedon* (text-fig. 5) show that most were fossilized flattened in a horizontal plane, although it is hard to say whether they are lying on their bellies or on their backs. Only the type specimen lies partially on its side (text-fig. 5A). The vertebral column is usually unbroken and the ribs and gastralia retain their associations. The limbs are often in a natural resting pose, with the forelimbs flexed and pointing forwards, the hindlimbs pointing forwards or backwards. The shoulder girdle and pelvis may retain their original positions, but they usually collapse. The skull is often present undamaged and in close articulation with the vertebral column. In these specimens there is no evidence of disarticulation by water currents, wind, or moving sand. The animals generally appear to have died naturally and to have been covered by sand fairly rapidly. One or two isolated bones, such as tooth-bearing elements (EM 1926.6; BMNH R3151, R4780; MM L8272), show that some skeletons were broken up before fossilization.

The remains of the other medium-sized reptiles, *Stagonolepis* and *Ornithosuchus*, are also generally preserved with vertebrae, limbs, and skull in articulation. Even the double row of dermal scutes above the vertebrae of *Ornithosuchus* often occurs in its original position. However, scutes of *Stagonolepis* are very often found isolated, and small bones may be slightly scattered in some cases (e.g. foot of *Ornithosuchus*: Walker 1964, p. 95). The type specimen of *O. woodwardi* (BMNH R2409–2410) is preserved with the skeleton lying on its side and the skull in a horizontal plane. The head is turned back close to the sacrum presumably by drying out of the neck ligaments after death. The



TEXT-FIG. 5. Skeletons of *Hyperodapedon* as preserved to show typical positions of fossilization. Vertebrae and ribs are shaded black, and all other elements are shown in outline. A, EM 1978.566.1–2; B, EM 1978.567.1–3; C, EM 1886.3 (dorsal slab); D, BMNH R699 (dorsal slab); E, BMNH R4782 (from casts); F, BMNH R4791/4805 (from casts); G, RSM 1967.10.1 (from casts).

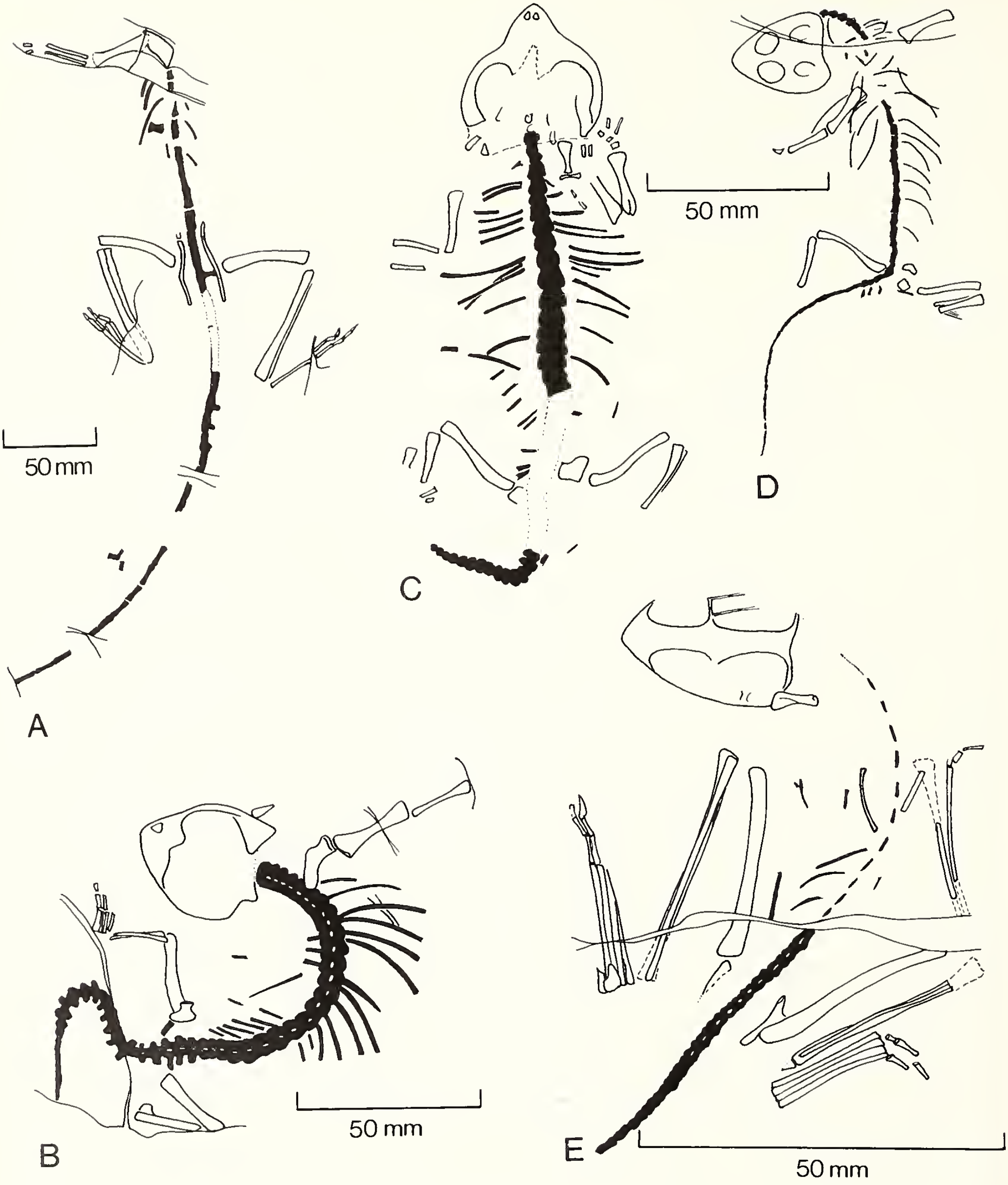
Ornithosuchus skull, BMNH R3143, is preserved on its side. However, it should be stressed that there are no complete specimens available of *Stagonolepis* or *Ornithosuchus*. In fact, only a few specimens of *Stagonolepis* show more than a small group of associated bones, and it is clearly not possible to say a great deal about the attitude and completeness of the specimens. The main reasons for the lack of complete specimens were that there was usually no one with sufficient professional interest around at the time of discovery to make sure that everything was picked up, and it was clearly difficult to collect large fossils which were preserved as moulds in a virtually structureless sediment. This is particularly true of *Stagonolepis* which also had hundreds of scutes around its body: these would have made careful collection even more difficult. Many scutes were doubtless removed from their proper association because they made attractive specimens on their own. Only specimens of *Stagonolepis* and *Ornithosuchus* from Findrassie show signs of transport. They are disarticulated and slightly damaged, and Walker (1961, p. 106) noted that pebbles are occasionally present in the Findrassie matrix. These facts may indicate some reworking by water.

The small reptiles of the Lossiemouth Sandstone Formation (*Leptopleuron*, *Scleromochlus*, *Saltopus*, *Brachyrhinodon*) are often preserved in an undisturbed well-articulated state and flattened in a horizontal plane (text-fig. 6). The skull is in place, the backbone may be straight or curved, and the limbs are in a natural squatting pose, as with the specimens of *Hyperodapedon*. However, there are about ten partial skulls of *Leptopleuron*—isolated mandibles, maxillae, parts of the cheek region. In one specimen the skull roof behind the orbits has been lost, and probably also the upper part of the braincase. One *Brachyrhinodon* has also lost the skull roof. The type specimen of *Erpetosuchus* (BMNH R3139) has the jaws wide open and the forelimbs in a 'standing' pose. Two individuals of *Scleromochlus* are preserved together on one slab (BMNH R3146) with the head of one lying partly over the anterior trunk of the other.

In detail most bones are excellently preserved and they show little sign of crushing or compression. Larger limb bones, however, are more likely to be crushed or distorted, even in association with other unaffected elements. A right ilium (BMNH R4788) and a posterior caudal vertebra (GSM 90884) of *Stagonolepis* became distorted without fracturing, and this led to problems of identification (Walker 1961, pp. 106–107). A skull of *Ornithosuchus* (BMNH R3142) was compressed in such a way that the orbit was reduced to half its original height, and the jugal was distorted (Walker 1964, pp. 58–61). The shoulder girdles of two specimens of *Hyperodapedon* (BMNH R4782; RSM 1967.10.1A) are rather compressed (text-fig. 7A, B), and the skull of BMNH R4782 has also collapsed slightly. The compression of all of these bones has probably been caused by the weight of superincumbent sediment, unusual in a sandstone matrix. Delicate skulls, like those of *Scleromochlus*, may be completely flattened. Various specimens of *Hyperodapedon* (e.g. BMNH R4782; RSM 1967.10.1A, 2; GSM 90932/5) show fine cracks or larger fractures on the surface of the bone (text-fig. 7C) which may be connected with the same process. The cracks have not opened in any way, and they are probably not suncracks.

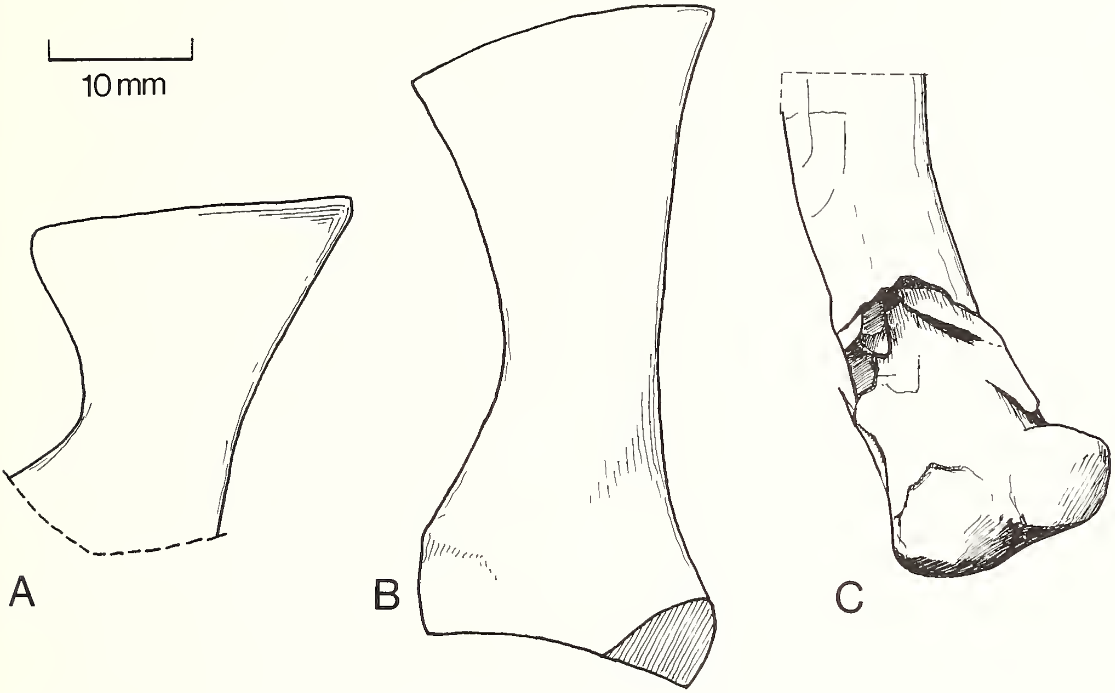
Signs of predation or scavenging appear to be rare, but this is hard to assess because of collection failure in many cases. Walker (1964, pp. 129–131) described a specimen of *Ornithosuchus* (BMNH R3562) in which an articulated skeleton of a large individual has been crushed and broken in certain areas. The anterior scutes of the left side are damaged, the transverse processes of the associated vertebrae are broken off short, the anterior edge of the left scapula, which lies immediately below these vertebrae, is also broken and incomplete. The humerus is broken at the same point and the ribs of the left side are missing. The body has been considerably disturbed in the region of the left shoulder and side, but the rest of the skeleton is not affected, so that the damage was almost certainly caused by a predator or scavenger.

Two isolated skulls of *Hyperodapedon* (RSM. GY.1984.20.1, 2) show similar localized damage. In one the parietal is broken off just behind the attachment of the epipterygoids, and small displaced bone chips are preserved, and the top of the braincase is slightly crushed. This damage occurred before fossilization and probably at, or after, death since the breaks are clean, but there are no tooth or claw marks on the bone. The damage was probably not caused by physical processes since fine sclerotic plates are preserved, only slightly displaced, in the orbit. In the other specimen the braincase



TEXT-FIG. 6. Skeletons of some smaller reptiles from the Lossiemouth Sandstone Formation to show the positions of fossilization. Vertebrae and ribs are shaded black, and all other elements are shown in outline. A, *Saltopus*, BMNH R3915 (ventral slabs); B, *Leptopleuron*, EM 1978.718 (from casts); C, *Leptopleuron*, EM 1920.5 (from casts); D, *Brachyrhinodon*, BMNH R4776 (dorsal slab); E, *Scleromochlus*, BMNH R3556 (from casts).

has been completely removed, and it is represented by only two fractured, displaced bone slivers. The atlas, axis, and two anterior cervical vertebrae are preserved in articulation, but pushed in between the quadrates. Ossified hyoid elements are preserved in place, so the disarticulation is unlikely to have been caused by sedimentary processes.



TEXT-FIG. 7. Compression and pre-fossilization damage to bones of *Hyperodapedon* from the Lossiemouth Sandstone Formation. A, lateral view of a distorted partial left scapula, BMNH R4782 (cast), compared with B, lateral view of a left scapula, restored from casts of EM 1886.3 and BMNH R4795, both from animals of similar size; C, crushed distal end of a femur (cast of GSM 90932/5), showing pre-fossilization damage.

The bone material is either absent (some Findrassie specimens), or very soft and sometimes partly replaced by iron oxide (goethite) and fluorite (Spynie, Lossiemouth). When original material is preserved the structure of bones and teeth may be extremely clear, and the cavities highlighted by the replacement minerals. However, the bones are often preserved as natural moulds in very well-cemented sandstone. Positive preparation has proved to be difficult in most cases, although it has yielded useful information in the study of some specimens of *Stagonolepis* and *Ornithosuchus*. Normally, casts have been made from the natural moulds left as cavities in the rock, and various methods that involve flexible synthetic 'rubbers' have been developed in order to preserve the rock mould and produce a high-fidelity copy of the bone (Walker 1961, 1964, 1973; Benton and Walker 1981).

ECOLOGY OF THE LOSSIEMOUTH SANDSTONE FAUNA (text-fig. 8)

The composition of the fauna of the Lossiemouth Sandstone Formation and the average sizes of its constituents are summarized in Table 2. The absence of plants, invertebrates, and fish, and the relatively small numbers of specimens make it futile to draw up food-chains and calculate biomass and productivity.

Stagonolepis and *Hyperodapedon* dominate the fauna as medium-sized herbivores that must have fed in relatively well-vegetated and watered areas distinct from the dune-fields in which they are preserved. *Stagonolepis* had strong dorsal and ventral armour and a heavy tail. It may have grubbed for plants or invertebrates with its shovel-like snout, and masticated them with its small pointed teeth by means of a slicing jaw action. The structure of the forelimb and shoulder girdle show that *Stagonolepis* normally walked on all fours, and the forelimb may have been used for digging also. For fast movement it may have been able to hold its limbs under the body for short periods, as in crocodiles. *Stagonolepis* was a thoroughly terrestrial animal (Walker 1961).

TABLE 2. The Lossiemouth Sandstone Formation fauna: composition. Information from Walker (1961, 1964), Benton (1977, 1983*d*), and original. Material is listed in the Appendix.

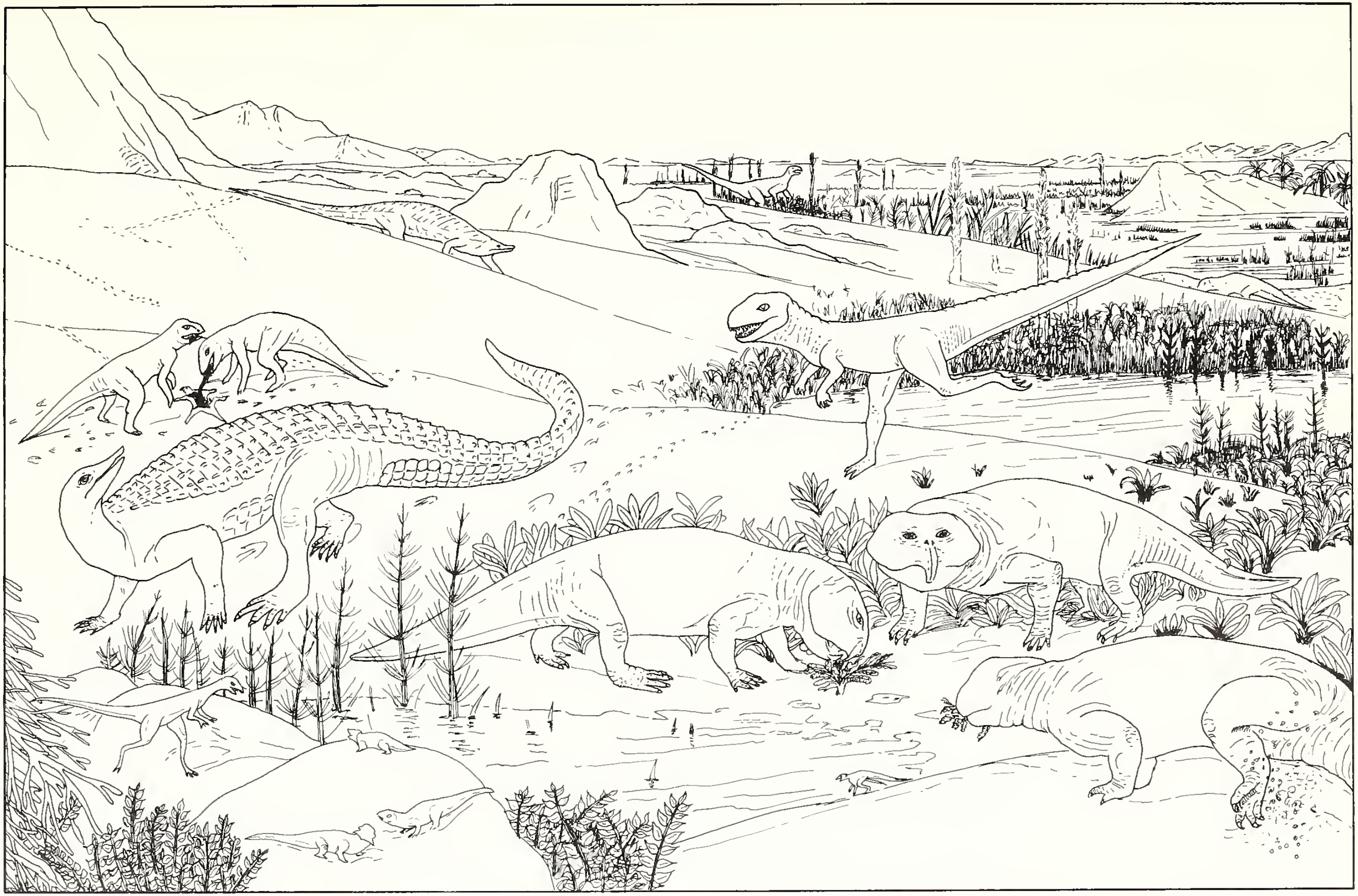
	Body length	Approx. number of individuals
Herbivores		
Stagonolepis	2·1–2·7 m	30(+)
Hyperodapedon	1·0–1·5 m	35
Carnivores		
Ornithosuchus	1·0–3·7 m	12
Saltopus	600 mm	1
Carnivore/insectivore		
Erpetosuchus	?700 mm	2/3
Small omnivores		
Leptopleuron	110–250 mm	?30
Brachyrhinodon	150 mm	?11
Scleromochlus	200 mm	7
		128

Hyperodapedon was a shorter more bulky terrestrial reptile which had powerful limbs. The massive laterally flattened claws of the foot and the construction of the hindlimb strongly suggest that it was used for scratch-digging. *Hyperodapedon* may have fed on buried roots and tubers and other low-level vegetation which it raked up with its premaxillary beak and manipulated with a large tongue. The jaws operated like a penknife, with the dentary cutting into a deep groove on the maxilla. There were multiple rows of teeth that were not replaced from below. There were massive spaces for adductor muscles at the back of the skull, and *Hyperodapedon* probably cut up tough plant material with a powerful precision-shear bite (Benton 1983*b*, *d*, 1984).

Stagonolepis and *Hyperodapedon* were probably preyed upon, or their carcasses scavenged, by large *Ornithosuchus*. *Ornithosuchus* may have been capable of bipedal locomotion for short spells, as well as quadrupedal locomotion. The long, curved teeth were clearly those of a carnivore, and the spinose scutes along the back may have been necessary for protection against cannibalistic attack (Walker 1964, 1977).

Erpetosuchus was a rare small carnivore and/or insectivore. The dentition was peculiar, with long sharp recurved teeth at the front of the jaws and toothless longitudinal ridges behind which may have been used for crushing the prey. There was also an incipient secondary palate, which may have been connected with the need to masticate the food.

Saltopus, Elgin's only dinosaur, was a small presumably carnivorous coelurosaur. It is more primitive than Huene (1910*a*) indicated, having three rather than four sacral vertebrae, and the anterior blade of the ilium is not very long. Further, *Saltopus* shows no particular adaptations to hopping, as he suggested. Huene also suggested that it had elongate cervical vertebrae, but these are not preserved: the anterior portion and the skull of the only skeleton is missing.



TEXT-FIG. 8. A scene at Elgin, north-east Scotland, in Lossiemouth Sandstone Formation times showing reconstructions of the reptiles in an imaginary scene with typical late Triassic plants. Three *Hyperodapedon* feed on seed-ferns in the foreground. Behind them an *Ornithosuchus* runs towards the armoured *Stagonolepis* which is looking over its shoulder. Behind *Stagonolepis* two *Erpetosuchus* feed on a small carcass. On the rocks in the left foreground are two *Leptopleuron*, a tiny *Brachyrhinodon*, and a small bipedal dinosaur, *Saltopus*. To the right of the rocks is the tiny *Scleromochlus* on the side of the pond. In and around the pond there are horsetails, cycads, and ferns, and there are tall lycopods in the distance. Based on a colour painting by Jenny Halstead in Benton (1983*b*).

Saltopus, small individuals of *Ornithosuchus*, and possibly *Erpetosuchus*, probably fed on the small herbivores of the Lossiemouth Sandstone Formation: *Leptopleuron*, *Brachyrhinodon*, and *Scleromochlus*. *Leptopleuron* may be seen as a 'reptilian rodent'. It had transversely broad back teeth consisting of two cusps linked by a narrow cross ridge, that were probably used for grinding up and chopping tough plants sliced off by its sharp, chisel-like front teeth. The teeth were set well forward in the jaws, the lower jaw was deep with a strong (coronoid) process, and the temporal area of the skull was broad, all of which suggests a very powerful jaw closing action. The back of the skull was spiny which may have acted to deter predators, to break up the outline of the animal against a background of spiny vegetation, and/or to form part of an interspecific combat display. The size and form of *Leptopleuron*, and its inferred habitat, are reminiscent of two desert-dwelling lizards: the Coast horned lizard, *Phrynosoma cornutum* from North America, and the Moloch, *Moloch horridus* from Australia.

Brachyrhinodon, a tiny sphenodontid with acrodont teeth on the jaw margins and on the palate, and a very short snout, was probably also a herbivore that could chop up tough vegetation with ease. It was much smaller than the living *Sphenodon* (*Brachyrhinodon* had a skull length of 20-30 mm; *Sphenodon* has a 70 mm skull), and its habits need not have been the same.

Scleromochlus is equipped with long hindlimbs that have been interpreted (Woodward 1907; Huene 1914) as adaptations to jumping, and it may have sought its food on the dunes in which it is preserved. Jumping animals (saltators) have lengthened hindlimbs, the distal segment in particular, several tarsal, or metatarsal, bones may lengthen, the tail is long (for balance), and the dorsal vertebral column may be shortened and the pelvis strengthened in order to withstand the impact of landing (Hildebrand 1974, pp. 512-515). *Scleromochlus* displays all of these features and in addition, it has a deep intercondylar fossa (patellar groove) at the distal end of the femur (Huene 1914, p. 10), a feature seen in jumping mammals to accommodate a strong quadriceps femoris tendon. *Scleromochlus* may be compared with the jerboa and kangaroo rat which are similarly adapted and live in hot, sandy deserts. The suggestion by Huene (1914) that *Scleromochlus* climbed trees and made 'bold leaps from a branch' or even glided, is not likely since the feet hardly appear to be adapted for grasping branches. Likewise, the suggestion by Wilfarth (1949, pp. 7-9) that *Scleromochlus* lived underwater and used its powerful hindlimbs to propel itself to the surface for air, seems even less probable! *Scleromochlus* also appears to have some specific adaptations for living on sand, like the North American desert-living iguanid lizards *Uma* and *Dipsosaurus*: the nares are nearly closed by lateral flanges, there is a posterior flange from the squamosal and quadratojugal protecting the tympanic region, the lower jaw is 'countersunk', and the metatarsus is flattened.

The sedimentological and taphonomic data suggest that most of the Lossiemouth Sandstone Formation animals normally lived in well-vegetated areas, possibly around interdune pools or close to water outside the dune-field. During arid periods, large sand dunes migrated across the floodplain, and many of the animals may have been overwhelmed by the sand. Others died from natural causes within the area of dunes. Nevertheless, it is striking that no fossils have been preserved in the underlying water-laid beds, of animals like fishes, labyrinthodont amphibians, or phytosaurs.

The cadavers were normally buried rather rapidly by drifting sand dunes, which is suggested by their relatively well-articulated state. There may have been some scavenging of the carcasses by *Ornithosuchus* and the smaller carnivores.

AGE VARIATION AND SEXUAL DIMORPHISM

Stagonolepis, *Ornithosuchus*, *Hyperodapedon*, and *Leptopleuron* are represented by enough specimens to permit some observations on variation in size and proportions.

The material of *Stagonolepis* segregates into two size groups, each containing similar numbers of specimens. Individuals within each group are remarkably uniform in size, and all measurements differ by 25-30% between the groups. Proportions are similar in both groups and morphological differences slight. These groups have been interpreted as male and female animals (Walker 1961). Romer and Price (1940) found two size-groups in material of *Dimetrodon limbatus* and they also explained these in terms of sexual dimorphism. Among living reptiles, male crocodiles and alligators tend to be larger than females of the same age (Guggisberg 1972, p. 127). Male lizards and tuataras also tend to be larger than females, but snakes often show exactly the opposite relationship (Goin and Goin 1971, pp. 115–116; Porter 1972, p. 309). Both situations may be found in chelonians.

Ornithosuchus displays a broad range of sizes, with estimated skull length ranging from 50 to 450 mm (Walker 1964, p. 57). These presumably represent age differences. A juvenile animal (BMNH R3149) shows proportional differences from larger specimens: relatively inflated cranium, short preorbital region, larger orbit, narrower interorbital region, upper temporal fossae diverge anteriorly and have a more medially placed process at the rear, and lack of posterior flanges of the parietals (Walker 1964, pp. 100–101).

The thirty-five specimens of *Hyperodapedon* display a range of sizes, with estimated skull length ranging from 125 to 210 mm, with the majority in the range 170–180 mm. One small fragment (RSM 1966.43.2) represents the tip of a juvenile dentary, but the other specimens cannot be segregated into distinct size-groups (Benton 1983*d*). Thus, as with *Ornithosuchus*, the size distribution corresponds to age alone. As is general among living reptiles, age size-classes may be apparent among juveniles, but they are usually blurred in older animals because of individual differences in growth rate (Gibbons 1976).

However, the material of *Hyperodapedon* may be divided into two classes according to proportions. For example, if two skulls of identical length are compared, certain 'important' elements (tooth-plate, occipital condyle, glenoid and quadrate facets) have the same dimensions, but bone bars and sheets between skull openings may differ markedly. Forms may be classified as 'gracile' or 'robust' on the basis of measurements of interorbital width, thickness of postorbital, or jugal, which differ by 20–70%. There is no relationship between these proportions and overall skull-size. It has been suggested (Benton 1983*d*) that the robust forms may be male, and the gracile forms female by analogy with certain living and fossil reptiles. The extant lizard *Lacerta jacksoni* shows sexual differences in the shape of the snout, nares, frontals, and occiput (Degen 1911). Proposed males and females of the dinosaur *Protoceratops* achieve the same maximum size, but differ in certain secondary sexual characters (frill, horn), as well as in the nasal height of the skull, size of the parietal fenestra, size of the nares, height of the coronoid process, and other features (Dodson 1976). Similarly, different skull patterns have been ascribed to sexual dimorphism in *Dimetrodon limbatus* (Romer and Price 1940), *Seymouria baylorensis* (Vaughn 1966), and *Tetragonias* (Cruickshank 1967).

Leptopleuron also shows well-marked 'robust' and 'gracile' forms independent of size. The type specimen (RSM 1891.92.528) is a small robust individual. These general findings in *Leptopleuron* are very similar to those in the related *Procolophon*. Broili and Schroeder (1936) found a range in skull sizes (lengths: 43–57 mm) and in robustness. The robust individuals had an additional horn-like process on the quadratojugal, and these were interpreted as males. There is some size variation in *Scleromochlus* also. Further study of the smaller Elgin reptiles is needed to establish the characters of age variation and sexual dimorphism.

DATING THE FAUNAS

The Hopeman Sandstone Formation

The footprints from the Hopeman Sandstone Formation (s.s.) are regarded as those of mammal-like reptiles, probably dicynodonts, and they closely resemble tracks from strata close to the Lower/Upper Permian boundary of Dumfriesshire, Penrith, and Mansfield (Hickling 1909; Watson 1909*b*; Watson and Hickling 1914; Haubold 1971; Smith *et al.* 1974). As noted already (p. 215), Glennie and Buller (1983) divided the Hopeman Sandstone Formation into two units, assuming that the contorted sandstones are confined to one horizon at about the same topographical level in the cliffs. However, since Williams (1973) recognized three well-separated horizons of contorted strata in upward succession from east to west, this assumption is open to question. Furthermore, the Clarkly Hill bore hole (Peacock *et al.* 1968, p. 130) encountered pebbly sandstone at the base of the Hopeman

Sandstone, many of the pebbles being faceted. This pebbly sandstone would naturally be taken to be the equivalent of the 'dreikanter bed' at the base of the Cutties Hillock Sandstone Formation, whereas Glennie and Buller correlate the upper of their two units with this formation. In addition, Glennie and Buller (p. 57) imply that the reptilian tracks occur in the lower of their two units, again if anything suggesting a correlation of this unit with the Cutties Hillock beds. The latter, however, are of very late Permian age. In fact, if we interpret Glennie and Buller correctly, the tracks would come predominantly from the upper of their two units, since they were most common in Masonshaugh, Greenbrae, and Clashach quarries. However, the evidence of the footprints cannot be regarded as very strong (see above), and the uncertainty over the succession within the Hopeman Sandstone Formation simply emphasizes the necessity for a separate Cutties Hillock Sandstone Formation in order to avoid confusion.

The Cutties Hillock Sandstone Formation

The reptiles from the Cutties Hillock Sandstone Formation were initially assumed to be of the same age as those from the Lossiemouth Sandstone Formation (Judd 1885, 1886*a*). However, Newton (1893) hinted that the faunas were distinct, and Taylor (1894) suggested a Permian age. Independently, Huene (1902) and Boulenger (1904) made the same suggestion. Walker (1973) discussed the age of the Cutties Hillock reptiles in detail, comparing *Elginia* and *Geikia* with animals from South Africa and Tanzania. He concluded that the Elgin formation was to be placed very close to the Permo-Triassic boundary, as had Watson and Hickling before him (1914), tentatively suggesting that it might lie at the very base of the Triassic, equivalent to a position low in the *Lystrosaurus* Zone of South Africa. The main evidence for this suggestion was that both *Elginia* and *Geikia* are more advanced than their closest relatives from the late Permian of South Africa and Russia, particular stress being laid on the specialization of the skull of *Elginia*. This view was not only based on the high degree of the spinescence, as stated by Rowe (1980), but reference was made to other skull characteristics. Rowe (1980) considered that the relationships of *Geikia* point to an uppermost Permian (i.e. *Daptocephalus* Zone) horizon for the Cutties Hillock Sandstone Formation. Using different evidence from that cited by Walker, Rowe confirmed that *Dicynodon locusticeps* (Huene, 1942), from the late Permian of Tanzania, is close to the ancestry of *Geikia*, and in fact referred *D. locusticeps* to the genus *Geikia*. He also showed that the close relatives of *Geikia*, the cryptodontid dicynodonts, all come from the late Permian of South Africa or Zambia. On the other hand, pareiasaurs less specialized in the skull than *Elginia* persist into the higher part of the *Daptocephalus* Zone (Kitching 1977), and there seems no reason why this group should have become extinct world-wide at the Permo-Triassic boundary. On balance, it seems best to take a conservative course, and regard the Cutties Hillock Sandstone Formation as lying at the extreme summit of the Permian, but bearing in mind that *Elginia* may represent a relict line which lingered on rather later in Scotland than elsewhere.

The Lossiemouth Sandstone Formation

The dating of the Lossiemouth Sandstone Formation has an even more involved history. The Elgin sandstones were all initially considered to be Devonian in age, until finds of reptile footprints and bones in the period between 1850 and 1860 convinced most palaeontologists that some of them must be regarded as younger. Local geologists long considered that the Lossiemouth sandstones were Devonian because they wanted to 'have' the oldest reptiles in the world (e.g. Phillips 1886; Gordon 1892). Also, certain geologists (e.g. Sir R. I. Murchison, Charles Lyell) had their own reasons for preferring to assign the reptiles to the Old Red Sandstone (Benton 1983*c*). However, Huxley (1867) argued convincingly for a Triassic age, and Murchison (1867, p. 267) accepted an Upper Triassic assignment.

Huene (1908) correlated the Lossiemouth sandstones with the German Lettenkohle (Late Ladinian) on the assumption that *Hyperodapedon* also occurred in the 'Lower Keuper' sandstone of the English Midlands together with amphibians and plants typical of the German formation.

However, the English material probably belongs to *Rhynchosaurus* (Walker 1969), and Huene's age assignment is not confirmed.

There is now strong evidence for a Lower Norian (Upper Triassic) assignment for the Lossiemouth Sandstone Formation. Walker (1961) pointed out that *Stagonolepis* is very closely similar to *Aetosaurus* from the German Stubensandstein (Middle Norian: Anderson and Cruickshank 1978; Tucker and Benton 1982). Aetosaurs occur also in the German Blasensandstein (*Ebrachosaurus* Lower Norian), the Dockum Group of Texas and the Chinle Formation of New Mexico and Arizona (*Desmatosuchus*, *Typothorax*: L.–M. Norian), the Maleri Formation of India (un-named: L. Norian), the Ischigualasto Formation and Los Colorados Formation of Argentina (*Aetosauroides* and *Neoaetosauroides*, respectively: L. Norian and U. Norian/Rhaetian), and the New Haven Sandstone of Connecticut (*Stegomus*: M. Norian). *Aetosauroides* is slightly more primitive than *Stagonolepis* (Walker, in discussion to Warrington 1970, p. 218). *Ornithosuchus* is most closely related to *Riojasuchus* from the Los Colorados Formation of Argentina (Norian: Bonaparte 1978). *H. gordoni* is remarkably similar to *H. huxleyi* from the Maleri Formation of India, and *Scaphonyx* from the Santa Maria Formation of Brazil and Ischigualasto Formation of Argentina (all late Carnian or early Norian). The Elgin procolophonid *Leptopleuron* appears to be very close to *Hypsognathus* from the Newark Group of New Jersey (latest Triassic or earliest Jurassic: Olsen and Galton 1977). *Brachyrhinodon* is most like *Polysphenodon* from the Gipskeuper (Carnian) of East Germany (Walker 1966). The other Elgin reptiles do not appear to have had close relatives elsewhere, as far as we know.

The close relationship of *Hyperodapedon* from Elgin and India is important. The Maleri Formation has also yielded a primitive phytosaur close to *Francosuchus* from the German Blasensandstein (Lower Norian). The Maleri Formation fauna also contains specimens of the labyrinthodont *Metoposaurus* which is restricted to horizons in Germany ranging from the Schilfsandstein to the Blasensandstein (Upper Carnian–Lower Norian). The Maleri Formation is very probably Lower Norian in age, and the Lossiemouth Sandstone Formation also. Unfortunately the age of the Lossiemouth beds cannot be confirmed independently by means of other fossil groups.

The Lossiemouth Sandstone fauna shows some affinity with other northern hemisphere faunas of the late Triassic. It shares aetosaurs, sphenodontids, procolophonids and, coelurosaurs with the North American and German faunas. However, the Elgin beds lack the metoposaur amphibians and phytosaurs that dominate all of these faunas. The other elements of the Lossiemouth Sandstone fauna show affinities with India and the southern continents: similar late Triassic rhynchosaurs are known from India and South America (a few scraps from North America), the closest relative of *Ornithosuchus* comes from South America, the South American and Indian faunas also have aetosaurs.

It is hard to find palaeogeographic reasons for these apparent distributional anomalies. The solution may depend on the environments in which the animals lived. The sediments in which the German, North American, and Indian faunas are found are largely water-laid, and metoposaurs and phytosaurs are clearly aquatic or semi-aquatic animals. However, the sediments of the South American formations are also largely water-laid, and amphibians are rare and phytosaurs are absent. The distinction between these two kinds of faunas is probably environmental, however, and they have been distinguished as a Metoposaur/Phytosaur Empire (Germany, North America) and a Rhynchosaur/Diademodontoid Empire (South America, ?Africa, ?India) (Tucker and Benton 1982; Benton 1983*a*). An interesting problem is the virtual absence of rhynchosaurs in North America, and their complete absence in Germany which is hard to explain in view of their overwhelming abundance elsewhere.

SUMMARY

1. Fossil reptile remains are known from four horizons in the region of Elgin, north-east Scotland: the Hopeman Sandstone Formation, the Cutties Hillock Sandstone Formation, the Lossiemouth Sandstone Formation, and the Rhaetic.

2. The remains from the Hopeman Sandstone Formation of the coastal region are footprints of several kinds. These indicate a range of two or three genera of mammal-like reptiles as the producers, and they resemble other mid- to late-Permian trackways from elsewhere.

3. The reptiles from the Cutties Hillock Sandstone Formation include two dicynodonts, *Geikia* and *Gordonia*, a pareiasaur, *Elginia*, and an un-named procolophonid. These reptiles indicate a date in the late Permian near the Permo-Triassic boundary.

4. The reptiles from the Lossiemouth Sandstone Formation include the rhynchosaur *Hyperodapedon*, the thecodontians *Stagonolepis*, *Ornithosuchus*, *Erpetosuchus*, and *Scleromochlus*, the procolophonid *Leptopleuron*, the sphenodontian *Brachyrhinodon*, and the early dinosaur *Saltopus*. These reptiles individually suggest a late Triassic age, and jointly a lower Norian age.

5. The reptiles from the Rhaetic of Linksfield include plesiosaurs and crocodiles, represented by odd teeth, vertebrae, and limb bones.

6. The Cutties Hillock Sandstone Formation is formally defined here, and it is distinguished from the Hopeman Sandstone Formation. There is little evidence for a direct correlation of the two, and the new name is required to show the distinctness of the two formations.

7. The reptiles of the Cutties Hillock Sandstone Formation and the Lossiemouth Sandstone Formation occur in aeolian sediments. The skeletons are preserved fairly completely, and with only occasional disturbance (by predators?). The bone is sometimes preserved, and sometimes completely lost, so that casts can be made. There is good evidence that the skeletons occurred low in their respective formations, at the base of large aeolian dunes.

8. The Lossiemouth fauna includes medium-sized herbivores that must have fed in well-watered areas, as well as smaller lizard-shaped animals that show adaptations for running around in the dunes. For some genera there are enough specimens to show age variation and sexual dimorphism.

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APPENDIX

Significant specimens of Elgin reptiles. Repository abbreviations are: BMNH, British Museum (Natural History); EM, Elgin Museum; GSE, Geological Survey Museum, Edinburgh; GSM, Geological Survey Museum, London; NUGD, Newcastle University, Geology Department; RSM, Royal Scottish Museum.

Hopeman Sandstone Formation footprints

Brickenden's (1850) slab: GSM 113445
Huxley (1859*b*, 1877): GSM (several slabs)
Undescribed: EM (6 slabs); RSM (several slabs); other material in Forres Museum; Inverness Museum and Manchester Museum

Cutties Hillock Sandstone Formation reptiles

Gordonia traquairi Newton 1893
  GSE 4805–4806, 11703 (type specimen); GSM 58313–58318 (casts from type); (?)EM 1978.550
Gordonia huxleyana Newton 1893
  GSE 4799–4802, 11704–11705 (type specimen); (?)EM 1978.549
Gordonia juddiana Newton 1893
  EM 1890.3 (type specimen)
Gordonia duffiana Newton 1893
  EM 1978.559.1, 2 (type specimen)
Geikia elginensis Newton 1893
  GSM 90998–91015 (type specimen)
'dicynodont' (?*Gordonia*)
  BMNH R4794; EM 1935.8, 1978.558, 886; RSM (Knock of Alves); RSM 1956.8.3, 1966.42.1–3, 1984.20.7
Elginia mirabilis Newton 1893
  GSE 4783–4788 (type specimen), 4780–4781, 4791; EM 1978.546, 547, 548; RSM 1956.8.1–2
procolophonid
  EM 1978.560; BMNH R4807(?)

Lossiemouth Sandstone Formation reptiles

Stagonolepis robertsoni Agassiz 1844
  EM 1858.10 (type specimen); other material is listed in Walker (1957, 1961), plus Manchester Museum L8265, L8267; RSM 1952.10.2, 1966.43.3, 9; Glasgow Museum, Kelvingrove G66, 41aj–as; Tübingen unnumb.
Hyperodapedon gordoni Huxley 1859
  EM 1978.566.1–2 (type specimen); other material is listed in Benton (1983*d*)
Ornithosuchus longidens (Huxley 1877)
  BMNH R2409–2410 (type specimen of *Ornithosuchus woodwardi*); EM 1978.570–571 (type specimen of *Dasygnathus longidens*); other material is listed in Walker (1964)
Erpetosuchus granti Newton 1894
  BMNH R3139 (type specimen); (?)RSM 1966.43.4; NUGD unnumb.
Saltopus elginensis Huene 1910
  BMNH R3915 (type specimen)
Leptopleuron lacertinum Owen 1851
  RSM 1891.92.528 (type specimen), 1966.43.7, 10; BMNH R3136, R3144,R3145, R3147, R3362, R3363, R3365, R3558, R3917, R3918, R3919, R3920, R3922, R3923, R3924, R3925, R3926, R3927, R3928, R3930, R3931, R4779; EM 1920.5, 1978.718, 726, 727.1–3; GSM (91079, 91082–91084, 91087–91088, 91093); RSM.GY.1984.20.34; Tübingen PV18415
Brachyrhinodon taylori Huene 1910
  BMNH R3559 (type specimen), R3364, R3921, R3929, R4776, R4777, R4778; EM 19–21 (+42?), 24–27, 30–31; RSM 1966.43.6, 8
Scleromochlus taylori Woodward 1907
  BMNH R3556 (type specimen), R3146, R3557, R2914, R4823, R4824, R5589
Unidentified thecodontian
  MM L8270

NOTE ADDED IN PROOF

The bone from Crownhead Quarry (see p. 217) is now numbered Forres Museum L1978-42ak. The footprint from Cutties Hillock figured by Watson and Hickling (1914, fig. 1) is in the Manchester Museum (MM L10275).

THE NAUTILOID *BRACHYCYCLOCERAS* IN THE UPPER CARBONIFEROUS OF BRITAIN

by D. PHILLIPS

ABSTRACT. The nautiloid genus *Brachycycloceras*, known from Pennsylvanian sediments in the U.S.A., occurs rarely in the British Isles where it is represented by two species *B. koninckianum* (d'Orbigny) and *B. obtusum* (Brown). These two species are re-described and synonymies suggested. The distinctions between *Brachycycloceras*, *Reticycloceras*, *Cornuella*, and *Perigrammoceras* are discussed briefly.

BRACHYCYCLOCERAS is a relatively well known orthoconic nautiloid in the Pennsylvanian rocks of the United States of America. Its occurrence in the Upper Carboniferous of the British Isles has not been widely recognized, hitherto. Previous references in the British literature to this genus have been to *Orthoceras koninckianum* d'Orbigny and *O. obtusum* Brown. Neither of these two species was included by Miller *et al.* (1933), nor by Furnish *et al.* (1962) in their descriptions of *Brachycycloceras*.

In this paper the affinities of *Brachycycloceras* to morphologically similar Carboniferous genera are briefly discussed. These include *Reticycloceras* Gordon, 1960; *Cycloceras* M'Coy, 1844 (= ?*Perigrammoceras* Foerste, 1924); and *Cornuella* Shimansky, 1968. The two British species of *Brachycycloceras*, *B. koninckianum* (d'Orbigny) and *B. obtusum* (Brown) are re-described and illustrated, and their affinities with North American species are discussed. Knowledge of the genus in the British Isles is limited by the paucity of suitably preserved specimens.

SYSTEMATIC PALAEONTOLOGY

Superfamily ORTHOCERATACEAE M'Coy, 1844
Family BRACHYCYCLOCERATIDAE Furnish, Glenister and Hansman, 1962
Genus BRACHYCYCLOCERAS Miller, Dunbar and Condra 1933

Type species. Brachycycloceras normale Miller, Dunbar and Condra, 1933 (? = *Orthoceratites koninckianum* d'Orbigny, 1850).

Diagnosis. Moderately large nautiloids consisting of rapidly expanding orthoconic to weakly cyrtoconic, exogastric, longiconic deciduous shell and breviconic truncated mature conch. Deciduous portion circular to quadrate in cross-section, strongly annulate, shell surface finely lirate; mature shell, weakly annulate to non annulate with lirate surface ornament. Mature shell with internal dorsal and dorso-lateral transverse thickened ridge and prominent bilobate muscle scars. Septa thin, directly transverse in deciduous portion but strongly directed to the anterior, dorsally in mature conch. Siphuncle between centre and venter, septal necks questionably suborthochoanitic.

Discussion. The genus was introduced by Miller *et al.* (1933) for a group of Pennsylvanian nautiloids distinguished by a rapidly expanding (1 in 3 to 5) orthoconic shell with subquadrate cross-section, irregularly spaced, prominent, sinuous annuli, and a finely lirate surface, represented by *B. normale* n. sp., *B. crebricinctum* (Girty), and *B. kentuckiense* n. sp. Including these latter species in the synonymy of *B. normale*, Furnish *et al.* (1962) were able to show specimens exhibiting an abrupt increase in the rate of expansion of the shell at a thickened septum of truncation on the formation of a breviconic ascoceroid-like mature body chamber. The siphuncle, situated between centre and venter, is said to have suborthochoanitic septal necks. The internal characters of the genus have not been well

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illustrated, and the observations made here are limited also by the paucity of British material and its preservation.

Brachycycloceras appears to be uncommon in Britain. The present account is based on examination of approximately twenty-four specimens in the collections of the British Museum (Natural History), the British Geological Survey, and the Manchester Museum. All the specimens of deciduous shell are fragmentary, lacking apical parts, and none shows the abrupt expansion into mature body chamber as illustrated by Furnish *et al.* (1962, pl. 179, figs. 2, 3). Shell truncation may have occurred more than once in the animal's development, but this cannot be demonstrated from the material available here.

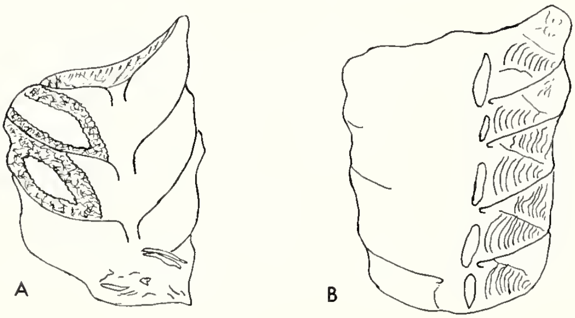
All except one of the mature body chamber specimens are referable to *O. obtusum* Brown. There is some resemblance to the type of *B. curtum* (Meek and Worthen), though the ventral expansion is not as great as that shown in plate 180, figure 3 of Furnish *et al.* (1962). One specimen (Pl. 24, figs. 6-8, 10) shows greater similarity to the mature *B. bransoni* (Miller and Owen) (Furnish *et al.* (1962), pl. 180, fig. 9), but it is only half the size. The deciduous portions of shell examined represent only the single species *B. koninckianum*, unless the interpretation of Phillips's figured specimens of *O. reticulatum* as pathological and *O. annulatum* as *Reticycloceras*, here given, is incorrect.

The information available on the age of the genus indicates a Namurian (E2) to Lower Westphalian A (G2) range. Records of specimens from the Dukinfield Marine Band, Westphalian B (Wright 1931, p. 148), and the Viséan P2 (Stephens *et al.* 1953, p. 12) are suspected of being misidentifications, though the specimens were not available for examination by the author.

The many unanswered questions concerning the genus *Brachycycloceras* are likely to remain until additional well-preserved and localized material is available for study.

Affinities. There seems to be sufficient variation in the external characters of the annulate orthocones that occur in the British Carboniferous, to enable distinction to be made between *Brachycycloceras*, *Reticycloceras* Gordon, 1960, '*Cycloceras*' M'Coy, 1844, and *Cornuella* Shimansky, 1968.

In *Reticycloceras*, the shell expands at a slower rate of 1 in 6·5 to 7·5. The cross-section is circular. Five to seven regularly spaced, sharply rounded annuli are present in a length equal to the diameter. They are slightly oblique to the long axis. The surface of the shell is coarsely lirate transversely and the juvenile shell is also longitudinally lirate before the appearance of pronounced annulation, producing a reticulate ornament (Pl. 25, fig. 1). This last feature is of doubtful significance generically, since fine reticulate ornament is present on the juvenile parts of several different nautiloid genera throughout the geological column. The siphuncle is subcentral, suborthochoanitic to weakly cyrtochoanitic with subcylindrical connecting rings (text-fig. 1B).



TEXT-FIG. 1. Drawings of median dorso-ventral sections. A, ?*Brachycycloceras* sp. BMNH C181. Apical part of specimen figured Plate 25, figs. 4-7, ×3. B, apical part of *Reticycloceras* sp. BMNH C31867, ×6. Carboniferous, Scotland.

The form commonly referred to *Cycloceras* or *Perigrammoceras*, i.e. *O. laevigatum* M'Coy (Foord (1897), p. 14, pl. 15, fig. 1*d*, *e*) is a gradually expanding (1 in 26) shell with a circular cross-section and a centrally situated orthochoanitic siphuncle. The annuli are prominent, broadly rounded, regularly spaced, directly transverse to the long axis, and without sinuosity. The surface is transversely lirate.

In *Cornuella* (e.g. BMNH 80385, C2884, C81323) the rate of expansion is about 1 in 6 and the shell is slightly cyrtoconic with a circular cross-section. The annuli are somewhat oblique to the long axis but without sinuosity, well rounded in cross-section and ribbed longitudinally.

Brachycycloceras koninckianum (d'Orbigny, 1850)

1844 *Orthoceras anceps* de Koninck, p. 517, pl. 45, fig. 7*a*, *b* (non Münster 1840).
1850 *Orthoceratites koninckianum* d'Orbigny, p. 113.
1905 *Orthoceras koninckianum* d'Orbigny; Hind, p. 111, pl. 5, fig. 22.
?1933 *Brachycycloceras kentuckiense* Miller, Dunbar and Condra, pl. 3, figs. 1, 2.
?1933 *Brachycycloceras normale* Miller, Dunbar and Condra, pl. 3, figs. 3–5.
?1962 *Brachycycloceras normale* Miller, Dunbar and Condra; Furnish, Glenister and Hansman, pl. 179, figs. 2–4; pl. 180, figs. 7–8.

Holotype. The specimen figured in pl. 45, fig. 7*a*, *b* of de Koninck (1844).

Material. Nine specimens in BMNH Coll. C5272, C27460, C28456, C78412, C78413, C78414, C85233–85234, C85235. Eight specimens in MM L10027, L10792*a–g*. Two specimens in B.G.S. 82288, XIII/6/11.

Diagnosis. *Brachycycloceras* with a rapidly expanding (1 in 3) annulate orthocone. Annuli prominent, obtusely rounded, almost directly transverse to long axis with shallow lateral sinuses. The interval between annuli is somewhat irregular, usually four annuli in a length equal to diameter. Shell slightly quadrate in cross-section. Exterior surface of shell finely lirate transversely. The siphuncle is situated between centre and venter.

Discussion. The specific name was introduced by d'Orbigny to replace *O. anceps* de Koninck, a name preoccupied by Münster (1840). This species was not referred to by Miller *et al.* (1933) when establishing the genus *Brachycycloceras*, nor by Furnish *et al.* (1962). De Koninck's figure, reproduced here (Pl. 25, fig. 16) appears to show external features typical of *B. normale*, and the two are probably conspecific.

Apart from a poorly preserved, crushed specimen in shale (C85235), the British specimens in the BMNH collection are all solid fragments of deciduous portions of the shell. They range in size from a half diameter fragment of 15 mm in length to a specimen 40 mm in length (C85233). None of these specimens shows evidence of the accelerated expansion of the shell at the formation of the mature conch, nor of the adapical part of the shell below a diameter of 9 mm. A juvenile specimen from Chokier, Belgium (BMNH 64813) with a minimum diameter of 3 mm, shows an abrupt increase in the rate of expansion at the appearance of annulation (Pl. 25, figs. 2, 3). No extreme apical parts are available to show if reticulate ornament was present as in *Reticycloceras* (Pl. 25, fig. 1). Longitudinal striation can be seen, in some specimens, on the crests of the dorso-lateral parts of the annuli (e.g. C78413) that are thought to be evidence of former muscle attachment areas. They can be seen on the specimen of *O. reticulatum* figured by Phillips (1836, pl. 21, fig. 11), and may be the 'reticulation with moniliform lines' to which he refers, but that Foord (1888, p. 108) thought 'cannot now be made out'. Comparable muscle scars are well seen in BMNH C75834 (Pl. 24, figs. 6–8) referred to under *B. obtusum*. In some specimens a conchal and/or dorsal furrow is well shown.

The fine liration of the shell exterior follows the same direction as the annuli. In some specimens (e.g. MM L10792*a*, Pl. 25, fig. 12) parts of the lirae overrun previously formed ones in parabolae as in *Neorthoceras* (see Sweet 1964, p. K258, text-fig. 186: 5*b*). This feature is seen in several orthoceratids of different ages and is probably evidence of repair of shell damage.

The septa of *B. koninckianum* appear to have been thin and fragile. Most of the specimens seen are non-septate body chamber fragments filled with shell debris and juvenile goniatites (e.g. BMNH C78412). Phillips's *O. reticulatum* (1836, pl. 21, fig. 11), here refigured (Pl. 25, figs. 4–7) is a septate specimen. A drawing of the dorso-lateral median section of its apical part is here reproduced as text-figure 1A and shows longer than average orthochoanitic septal necks, though *Brachycycloceras* is said to be suborthochoanitic. The rate of expansion in this specimen (1 in 6) is close to that of *B. longulum* Miller and Owen (1934), but the annulation is closer to that of *B. koninckianum*. However, since the dorsal and conchal furrows preserved on this specimen are not in one plane (Pl. 25, fig. 7), it is possibly a pathological example and not reliable evidence for the internal structure of the genus.

Another of Phillips's figured specimens, *O. annulatum* (1836, pl. 21, fig. 10) is here refigured (Pl. 25, figs. 8–10). It was referred to by Furnish *et al.* (1962, p. 1347) and shows a superficial resemblance to their pl. 179, figs. 11, 12, showing *B. curtum*. On closer examination this specimen shows fractures indicating that its apparent cyrtoconic form and its rapid expansion are the results of distortion due to crushing of an originally orthoconic shell. The annulations are more numerous, more regularly spaced, and more acute than in *Brachycycloceras*, and lack the characteristic lateral sinuses. It is possibly a species of *Reticycloceras*.

The specimen here figured as Plate 25, fig. 15 is the original of Hind (1905, pl. 5, fig. 22: *O. koninckianum*). The true rate of expansion is not seen as the specimen is broken along its length on one side. It probably comes from the upper part of the Foynes Shales of R1 age, and a specimen of *Reticuloceras reticulatum* (Phillips) is in the same piece of matrix. Most of the other specimens seen are poorly documented in respect of horizon and locality, but with the help of published references to *O. koninckianum* it is evident that the species ranges throughout the Namurian from E2. A specimen seen by the writer (F1231, C. P. Eardly Coll., Stoke Museum) came from the roof of the Crabtree Coal at Werrington Colliery, Stoke-on-Trent, indicating a lower Westphalian A, G2 age. Specimens of *O. koninckianum* recorded by Wright (1931, p. 148) (LT 1707–1773) from as high as the Dukinfield Marine Band (i.e. Westphalian B) were not located by the writer in the BGS Collection. Other specimens, not found, were recorded from Viséan P2 strata (Stephens *et al.* 1953, p. 12), but are possibly misidentified specimens of the group of '*O. laevigatum*' M'Coy.

Brachycycloceras obtusum Brown, 1841

1841 *Orthoceras obtusum* Brown, p. 219, pl. 7, fig. 36.
1938 *Orthoceras dilatatum* de Koninck; Demanet, p. 166, pl. 126, fig. 1.
non 1941 *Brachycycloceras dilatatum* (de Koninck); Demanet, p. 113, pl. 4, fig. 3.

Holotype. The specimen figured by Brown (1841, pl. 7, fig. 36) in the Manchester Museum L10026.

Material. BMNH C5276, C78415, C5271, C82538; BGS BB4178; MM L10027.

Diagnosis. *Brachycycloceras* with a slightly depressed brevicone, expanding from deeply rounded basal septum at a rate of 1 in 3 viewed ventrally and 1 in 4 viewed laterally. Contracting adorally to produce an ovoid shell. Surface non-annulate, with fine transverse lirae that form shallow sinuses laterally. Ornament becoming coarser and imbricate adorally. Septa directed sharply anteriorly in a broad saddle on the dorsum.

Discussion. The holotype (Pl. 24, figs. 1, 2) is the adapical portion of a mature body chamber that is abraded and crushed on the dorsal side. More completely preserved specimens (e.g. Pl. 24, fig. 4) show that slight contraction occurred adorally, producing a somewhat ovoid shape. None of the specimens shows more than two septa, and none shows the complete suture line clearly. Demanet (1938, p. 166, pl. 126, fig. 1) figured an example of this species as *O. dilatatum* de Koninck, and listed it

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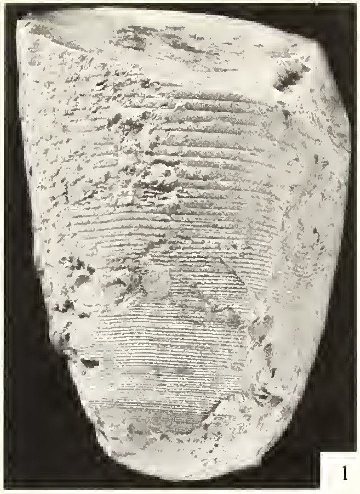
EXPLANATION OF PLATE 24

Figs. 1, 2. Holotype of *Orthoceras obtusum* Brown (1841, pl. 7, fig. 36). Manchester Museum L10026. Carboniferous, Hebden Bridge, Halifax, Yorkshire, × 1·5. 1, ventral view. 2, lateral view.

Fig. 3. *Brachycycloceras ?obtusum* (Brown). BMNH C5271. Hebden Bridge, Halifax, Yorkshire, × 1.

Figs. 4, 5, 9. *Brachycycloceras obtusum* (Brown). BMNH C5276. Carboniferous, nr. Halifax, Yorkshire, × 1. 4, ventral view. 5, lateral view. 9, apical view.

Figs. 6–8, 10. *Brachycycloceras* sp. BMNH C75834. Carboniferous, G1, Bankhall Colliery, Burnley, Lancashire. The periphract and retractor muscle areas have been outlined. 6, muscle scar, × 2. 7, dorsal view, × 1. 8, lateral view, × 1. 10, adoral view, × 1.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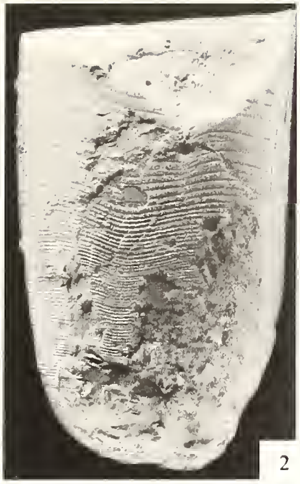
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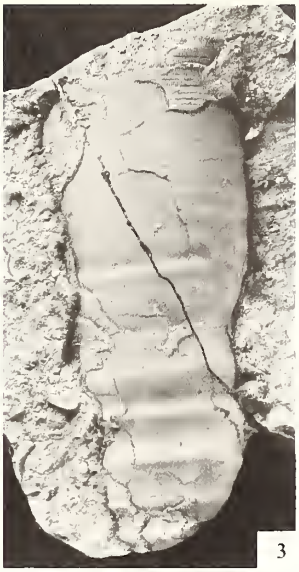
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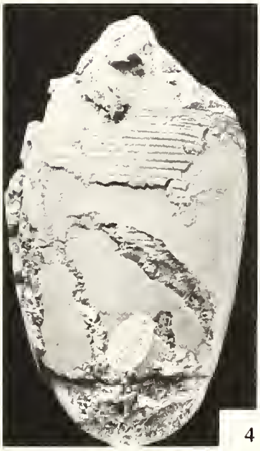
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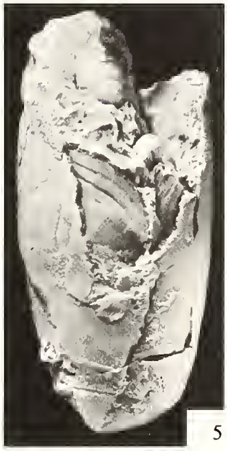
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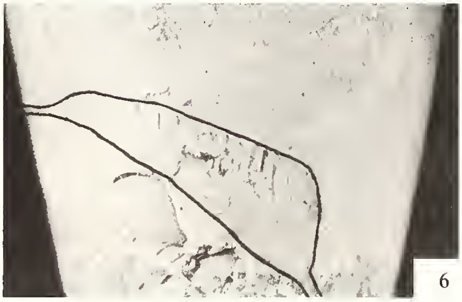
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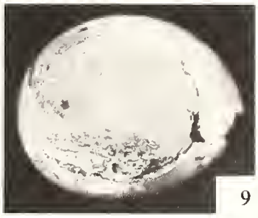
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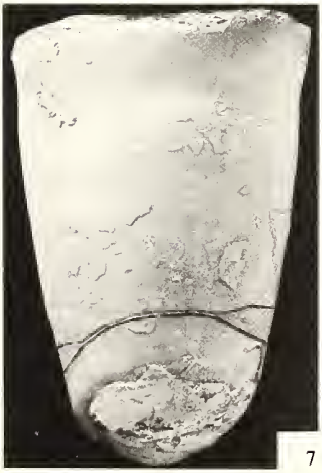
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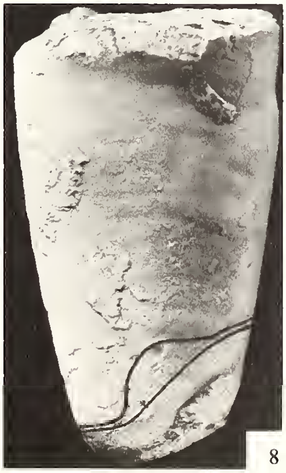
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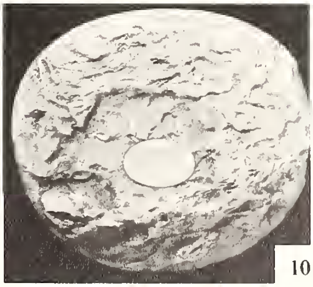
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PHILLIPS, *Brachycycloceras*

under the synonymy of *B. dilatatum* in his 1941 work. De Koninck's *O. dilatatum* is, however, a more rapidly expanding shell resembling the *B. curtum* of Furnish *et al.* (1962, pl. 180, figs. 1-4).

The basal septa of these specimens are strongly convex forward on the dorsum (Pl. 24, fig. 5) suggesting that they are mature decollated body chambers. Evidence for their inclusion in *Brachycycloceras* is poor in the absence of associated deciduous parts, but the lirate ornament of the shell is typical of that genus. One specimen (Pl. 24, fig. 3) that is probably referable to *B. obtusum* apparently shows a transition from strongly annulate deciduous shell to non-annulate mature body chamber with evidence of finely lirate ornament.

A different type of mature body chamber is shown by one specimen in the BMNH collection, C75834 (Pl. 24, figs. 6-8, 10). It shows closer resemblance to the *B. bransoni* (Miller and Owen) figured by Furnish *et al.* (1962, pl. 180, fig. 9) than to *B. obtusum*, though much smaller in size. It is a slightly depressed brevicone, expanding from 26 mm to 40 mm diameter in the lateral plane, and 24 mm to 35 mm dorso-ventrally, in a length of 60 mm. No evidence of annulation or surface ornament is preserved. The apex is damaged and obscured by matrix but the course of the suture can be made out. It is transverse across the venter and swings sharply forward on the lateral areas to form a broad, high saddle on the dorsum. Anterior of the apical septum, a dark brown band, 2 mm in width, encircles the shell parallel to the course of the septum, expanding on the dorso-lateral margins in small sub-ovoid areas with a conchiolin-like surface, slightly furrowed at the anterior margins. This is interpreted as representing the periphract and retractor muscle areas of attachment. A broad, shallow constriction runs transversely near the anterior margin dorsally, fading out dorso-laterally, indicating a corresponding thickened internal ridge of the shell.

The affinities of all these body chambers remains speculative in the absence of further well-preserved material, particularly of specimens showing deciduous and mature parts in association. Detailed horizon and locality information is also lacking for the *B. obtusum* specimens seen. Using published references—e.g. Wray *et al.* (1930, p. 34); Stephens *et al.* (1941, pp. 355, 360)—it can be seen that they occur through R1 and R2. BMNH C75834 is from the Union Mine Seam (i.e. G1), and a specimen is recorded by Stephens *et al.* (1953, p. 77) from the Pot Clay Marine Band (i.e. G2).

CONCLUSIONS

In Britain, examples of the nautiloid genus *Brachycycloceras* are of rare occurrence in Namurian and Westphalian A strata. The genus is recorded from higher levels in the succession in the U.S.A., being

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EXPLANATION OF PLATE 25

Fig. 1. *Retiycloceras* sp. juv. BMNH C71861. Carboniferous, nr. Dunfermline, Scotland, × 3.

Figs. 2, 3. *Brachycycloceras koninckianum* (d'Orbigny). BMNH 64813. Carboniferous, étage Houiller H, Chokier, Belgium, × 2.

Figs. 4-7. ?*Brachycycloceras* sp. BMNH C181 (= holotype of *Orthoceras reticulatum* Phillips, 1836, pl. 21, fig. 11). Carboniferous, Bolland, Yorkshire. Arrows indicate conchal and dorsal furrows. 4, ventral view, × 1. 5, ventral view showing conchal furrow, × 2. 6, dorsal view showing dorsal furrow, × 2. 7, apical view, venter uppermost, × 2.

Figs. 8-10. ?*Reticycloceras* sp. BMNH C206 (= *O. annulatum* Phillips, 1836, pl. 21, fig. 10). Carboniferous, locality unrecorded, × 1.

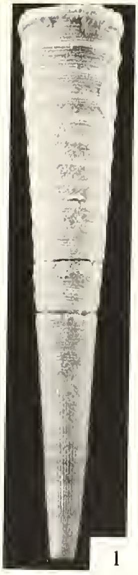
Fig. 11. Ventral view of *Brachycycloceras koninckianum* (d'Orbigny) showing conchal furrows (arrowed). Manchester Museum L10792*b*. Carboniferous, nr. Halifax, Yorkshire, × 1·2.

Figs. 12-14. *Brachycycloceras koninckianum* (d'Orbigny). Manchester Museum L10792*a*. Carboniferous, nr. Halifax, Yorkshire, × 2. 12, lateral view, parabolic ribbing shown on the adoral annulation. 13, ventral view. 14, apical view.

Fig. 15. *Brachycycloceras koninckianum* (d'Orbigny). BMNH C28456 (figured Hind (1905), pl. 5, fig. 22). Carboniferous, R1, Foynes Island, Co. Limerick, Eire, × 1.

Fig. 16. *Orthoceras anceps* as illustrated by de Koninck (1844, pl. 45, fig. 7*a*, *b*).

PLATE 25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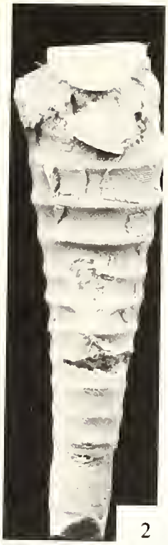
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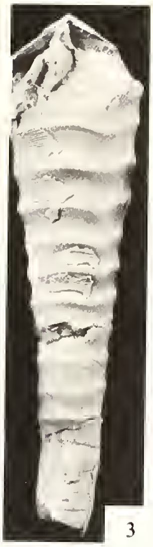
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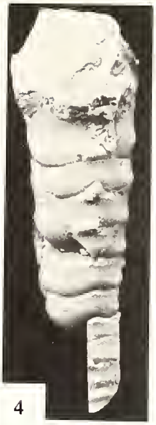
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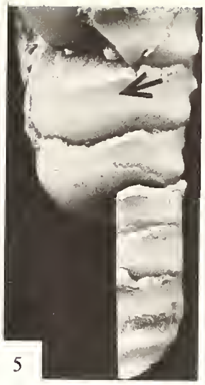
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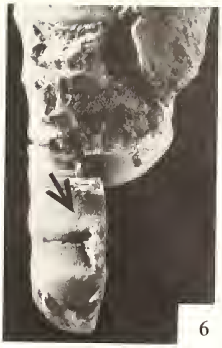
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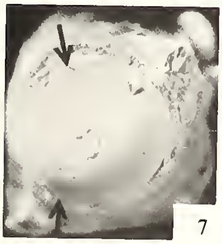
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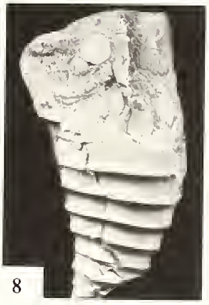
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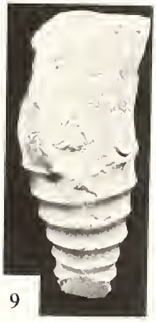
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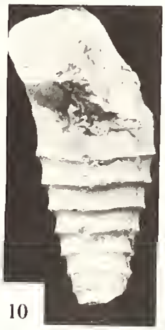
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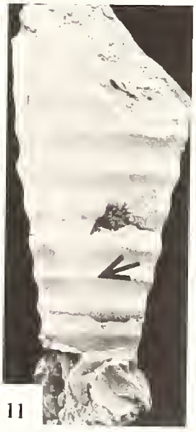
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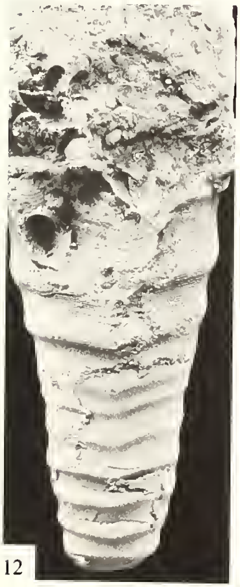
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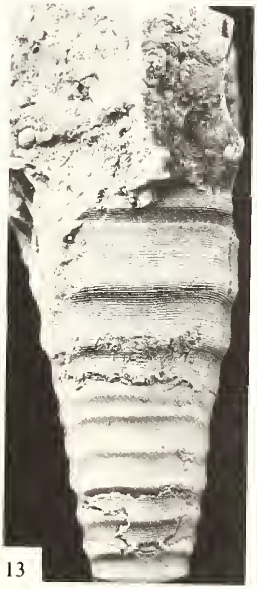
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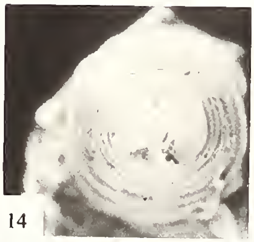
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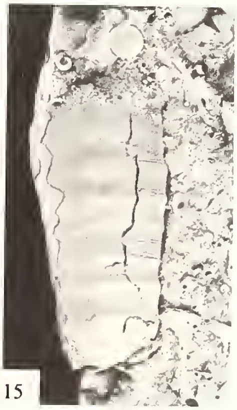
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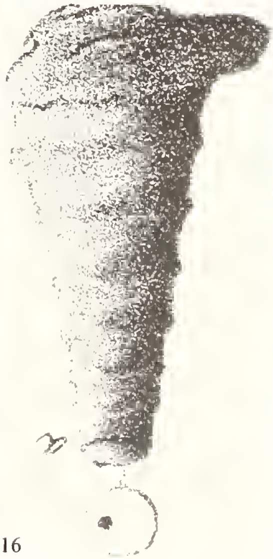
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PHILLIPS, *Brachycycloceras*

moderately abundant in Middle and Upper Pennsylvanian rocks. Fayetteville Shale (= Lower Namurian) specimens are described as *B. washingtonense* by Gordon (1964). Insufficient material is currently available from the British Carboniferous to enable a satisfactory delimitation of species, their development, and affinities.

Acknowledgements. I wish to thank Dr. R. M. C. Eager for facilitating examination of specimens in the Manchester Museum collection and for kindly providing photographs. My thanks go, also, to Dr. W. H. C. Ramsbottom and N. Riley for allowing me to examine BGS specimens. I am particularly grateful to my colleagues Drs. H. G. Owen and M. K. Howarth for helpful suggestions and discussion, and for reading the original manuscript.

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THE TAXONOMY, SHELL STRUCTURE, AND PALAEOECOLOGY OF THE TRIMERELLID BRACHIOPOD *GASCONSIA* NORTHROP

by NILS-MARTIN HANKEN *and* DAVID A. T. HARPER

ABSTRACT. The large trimerellid brachiopod *Gasconsia* Northrop is reassessed on the basis of the type species and abundant, well-preserved material from the upper part of the Bønsnes Formation (Rawtheyan: Ashgill Series) in the Ringerike district of the Oslo Region. Hitherto the genus was known only from indifferently preserved moulds from the upper Silurian of Quebec. The Norwegian specimens are assigned to a new species, *G. worsleyi*, and include valve interiors which permit a detailed analysis of the articulation and musculature. The shell has been replaced by sparry calcite which also characterizes the shells of the associated gastropods and cephalopods. This confirms the assumption that trimerellid brachiopods originally possessed an aragonitic shell. The unusual fauna containing *Gasconsia* in Norway is of low diversity and comprises articulate brachiopods, bryozoans, trilobites, ostracods, gastropods, corals, and calcareous algae. It is suggested that *Gasconsia* may have adopted a quasi-infaunal mode of life.

INTRODUCTION

TRIMERELLID brachiopods are rare in most Ordovician and Silurian faunas. Despite the detailed monographic study of the group by Davidson and King (1874) the internal features, for example the musculature and articulation, are poorly understood and not known in the majority of genera (Rowell 1965). To date the best preserved specimens of the Trimerellacea are incomplete silicified valves of *Dinobolus* from the middle Silurian of British Columbia described by Norford (1960) and *Eodinobolus* from the Caradoc of Fort Chute, Ontario, described by Norford and Steele (1969). Both studies revealed in detail internal features of the shells whilst the latter account speculated upon a viable mechanism for the relative movements of the valves.

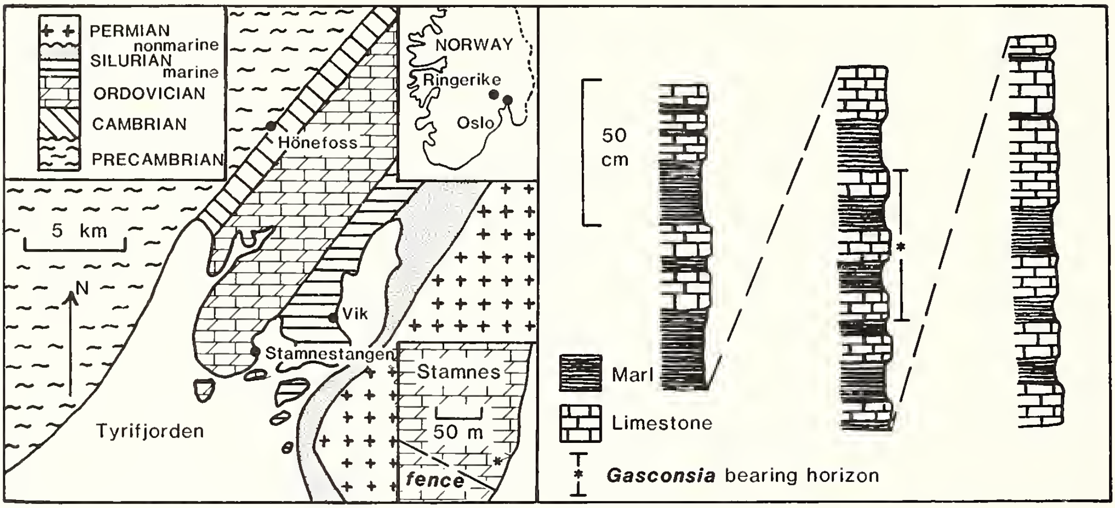
The genus *Gasconia* was erected by Northrop (1939, p. 161) on the basis of several indifferently preserved moulds from the upper Silurian Gascons and Bouleaux formations of the Gaspé peninsula, Quebec. Although no valve interiors were described by Northrop, he provisionally referred the genus to the Trimerellidae, whilst noting the similarity of the Canadian material to *Dinobolus transversus* (Salter) from the Wenlock of England. Rowell (1965, p. H863) was uncertain as to both the status and affinities of *Gasconsia*. However, during the course of this study a slab containing topotype specimens has been located in the collections of the Peabody Museum with a number of valve interiors displaying features comparable with those of the better preserved Norwegian species. The generic validity of *Gasconsia* therefore is confirmed by both the Canadian and Norwegian samples whilst Northrop's assignment of the material to the Trimerellidae is correct.

Abundant and well-preserved shell and mould material of a new species of *Gasconsia* from the upper Ordovician rocks of the Oslo Region provides detailed information on the trimerellid musculature and articulation and permits a new interpretation of their functional morphology. The existing fabric of sparry calcite and the indications of an original structure of lamellae confirms the assumption that the trimerellid shell was initially aragonitic (Jaanusson 1966). The Norwegian species, *G. worsleyi* is described whilst the type species *G. schucherti* is redescribed from type and topotype specimens.

G. worsleyi is known from a few beds of limestone within a thick sequence of limestones and marls towards the top of the upper Ordovician Bønsnes Formation, near Stamnestangen (= Stavnestangen)

[Palaeontology, Vol. 28, Part 2, 1985, pp. 243–254.]

in the Ringerike district of the Oslo Region (text-fig. 1). Ringerike is the sixth of Størmer's districts of the region (1953, fig. 1) and is situated some 40 km north-west of the capital city. The gently folded Lower Palaeozoic succession youngs to the south-east and is best exposed around the margins of the Tyrifjord. Although the Ordovician succession is virtually complete only the upper Caradoc and Ashgill formations have been described in detail; Hanken and Owen (1982) summarized previous research. The Bønsnes Formation occurs near the top of the Ordovician succession and is correlated with the Rawtheyan Stage of the Ashgill Series (Owen 1979). The formation is well exposed around the Bønsnes peninsula, particularly at and near Stamnestangen. Here Professor Kiær collected in excess of fifty individuals of the trimerellid. Further collecting by the authors has confirmed Kiær's locality information (text-fig. 1).



TEXT-FIG. 1. Simplified geological map of the Ringerike district showing *Gasconsia* locality at Stamnestangen; measured profile at NM 6816.5961 indicates extent of the *Gasconsia* bearing horizon.

TECHNIQUES

In contrast to the poorly preserved moulds of *G. schucherti*, the valves of the Norwegian *Gasconsia* are preserved in a matrix of microspar with small amounts of clay and silt grade terrigenous material. Quantitative analysis of the calcium carbonate, following the procedure of Dreimanis (1962), has indicated a content of about 90% in the *Gasconsia* bearing horizon. Information regarding the shell interiors was derived by selective dissolution of the shell material. However, due to the small difference in carbonate content between the fossils and the matrix, over-etching of the limy moulds poses a serious problem. The best results were obtained if the moulds were exposed to 5% hydrochloric acid for a maximum of about two minutes. After etching the specimen was dried, and the newly exposed part of the mould impregnated with a solution of pioloform in alcohol. When the alcohol has evaporated the pioloform precipitates, thus causing surface particles to adhere. This thin skin is fairly impermeable and prevents further etching. The dissolution/impregnation process was repeated until all the shell material was dissolved and the pioloform impregnated mould was then cast in silicone rubber.

The fauna from the marly horizons, between the *Gasconsia* bearing strata, was recovered from a number of different levels. The marl weathers fairly easily under natural conditions, and samples with a mean weight of about one kilogram were collected from especially well-weathered beds. To achieve further breakdown of the matrix the marl was treated with petrol following the procedure of Allman and Lawrence (1972). After treatment the material was screened according to grain size and the samples were picked for fossils larger than 0·5 mm.

Petrographic observations were made from thin sections without cover glass. For the study of the microstructures of the shells a Nuclide Luminoscope mounted on a Leitz petrographic microscope was used making it possible to study the thin sections both by standard light-microscopy and by cathodoluminescence. For the latter a beam current of 0·7–0·9 mA at 13–14 kV and 50 torr vacuum was used.

The measurement, statistical, and photographic techniques used in this study are those described in Harper (1984) except where stated otherwise.

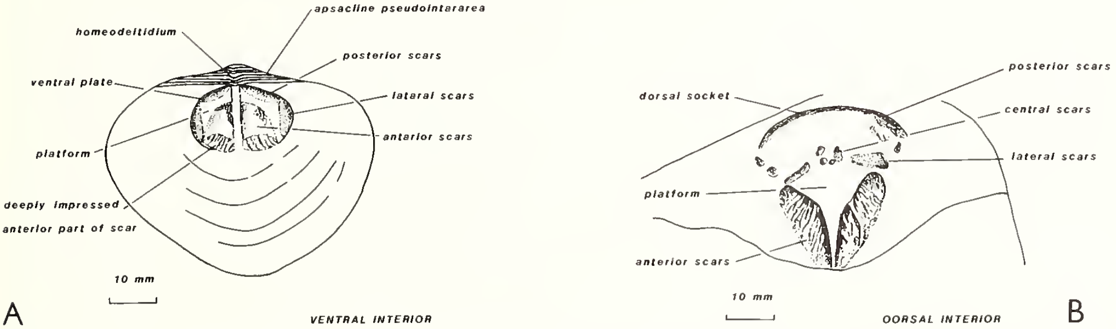
Repositories of specimens: PMO—Paleontologisk museum, Oslo; YPM—Peabody Museum, Yale University, New Haven.

SYSTEMATIC PALAEONTOLOGY

Superfamily TRIMERELLACEA Davidson and King, 1872
Family TRIMERELLIDAE Davidson and King, 1872
Genus GASCONSIA Northrop, 1939

Type species. By original designation, *G. schucherti* Northrop, 1939, p. 161; from the Gascons and Bouleaux formations (upper Silurian), Gaspé, Quebec, Canada.

Diagnosis. Large convexiplane to convexiconcave trimerellid of transversely suboval outline; dorsal and ventral platforms low, not vaulted and median ridges feeble or absent. Articulation achieved by curved ventral plate and corresponding dorsal socket. Ornament of locally thickened concentric growth lines and fine ribs usually restricted to inner shell layers.



TEXT-FIG. 2. *G. worsleyi* sp. nov. A, ventral interior, based on PMO 13091. B, dorsal interior, based on PMO 104.000

Remarks. Although the external diagnostic features of the genus are apparent in both *G. schucherti* and *G. worsleyi*, detailed data regarding the valve interiors were compiled from examination of the latter. Both known species of *Gasconsia* are large with well-defined ornaments of thickened concentric growth lines locally appearing as rugae. A small pooled sample of unbroken specimens of both species was investigated for size-independent morphological differences using Principal Components Analysis. *G. schucherti* consistently has a more transverse outline than that of *G. worsleyi*. Details of this analysis are housed with the figured material. *Gasconsia* is most similar to *Eodinobolus* in that both possess solid, not raised or vaulted platforms in both valves. *Eodinobolus*, however, possesses a different mode of articulation whereby a dorsal tooth fits into a ventral socket; furthermore the valves are relatively smaller and are subequally biconvex.

The large genera which characterize the Silurian trimerellid faunas, *Trimerella*, *Dinobolus*, *Monomerella*, and *Rhynobolus*, are subequally biconvex and possess raised or vaulted platforms in both valves. With the exception of *Dinobolus*, which possesses a dorsal plate and ventral socket, the articulating mechanisms of these genera are not well documented. None of the five trimerellid genera—*Sinotrimerella*, *Palaeotrimerella*, *Machaerocolella*, *Fengzuella*, and *Paradinobolus*—recently described from supposed early Caradoc rocks in western Zhejiang, China (Li and Han 1980) is comparable with *Gasconsia*.

Gasconsia schucherti Northrop, 1939

Text-fig. 4B–G

1939 *Gasconsia schucherti* Northrop, p. 161, pl. 12, figs. 6–8; pl. 13, fig. 7.

Material. Ten brachial and three pedicle valves; most are broken.

Lectotype. Selected herein, a pedicle valve YPM 13313A.

Diagnosis. A transverse *Gasconsia* species with about twelve ribs per 10 mm at the 30 mm growth stage and about 5–6 thickened concentric growth lines at a similar place.

Description.

Exterior. Very large convexiplane to convexiconcave valves of transverse outline with maximum width at or near mid-valve length; cardinal extremities obtuse and rounded. Anterior commissure rectimarginate. Pedicle valve about three-fifths as long as wide, roughly flat or weakly concave in both profiles but with local undulations; pseudointerarea short and apsacline with faint closely spaced growth lines. Brachial valve about three-fifths as long as wide and about one-fifth as deep as long. Anterior profile strongly but evenly convex with maximum convexity medianly; flanks feebly concave. Pseudointerarea reduced or obsolete. Lateral profile with greatest convexity over posterior third of valve surface; profile flattens slightly anteriorly. Ornament of thickened growth lines locally developed as rugae; about 5–6 per 10 mm are present medianly at 30 mm growth stage. Radial ornament of fine costae and costellae with uniformly rounded profiles apparently restricted to inner shell surfaces with about twelve per 10 mm medianly at 30 mm growth stage.

Valve interiors. Platforms and muscle scars poorly defined. Ventral interior with low, curved ventral plate and solid platform situated anteriorly; muscle scars not well defined. Dorsal interior with well-defined dorsal socket and bipartite, solid platform. Pair of oval anterior scars situated lateral to triangular anterior part of platform.

Remarks. Information regarding the valve interiors of *G. schucherti* is rather meagre but is sufficient to associate the Canadian species with the better preserved Norwegian material. *G. schucherti* possesses a dorsal socket and ventral plate together with solid platforms in both valves. The convexiplane valves are large and ornamented by rugae and ribs on their inner surfaces. These features characterise the genus and together they separate *Gasconsia* from all other trimerellid genera.

Gasconsia worsleyi sp. nov.

Text-figs. 3A–H; 4A, 2A, B

Derivation of name. For Dr. David Worsley.

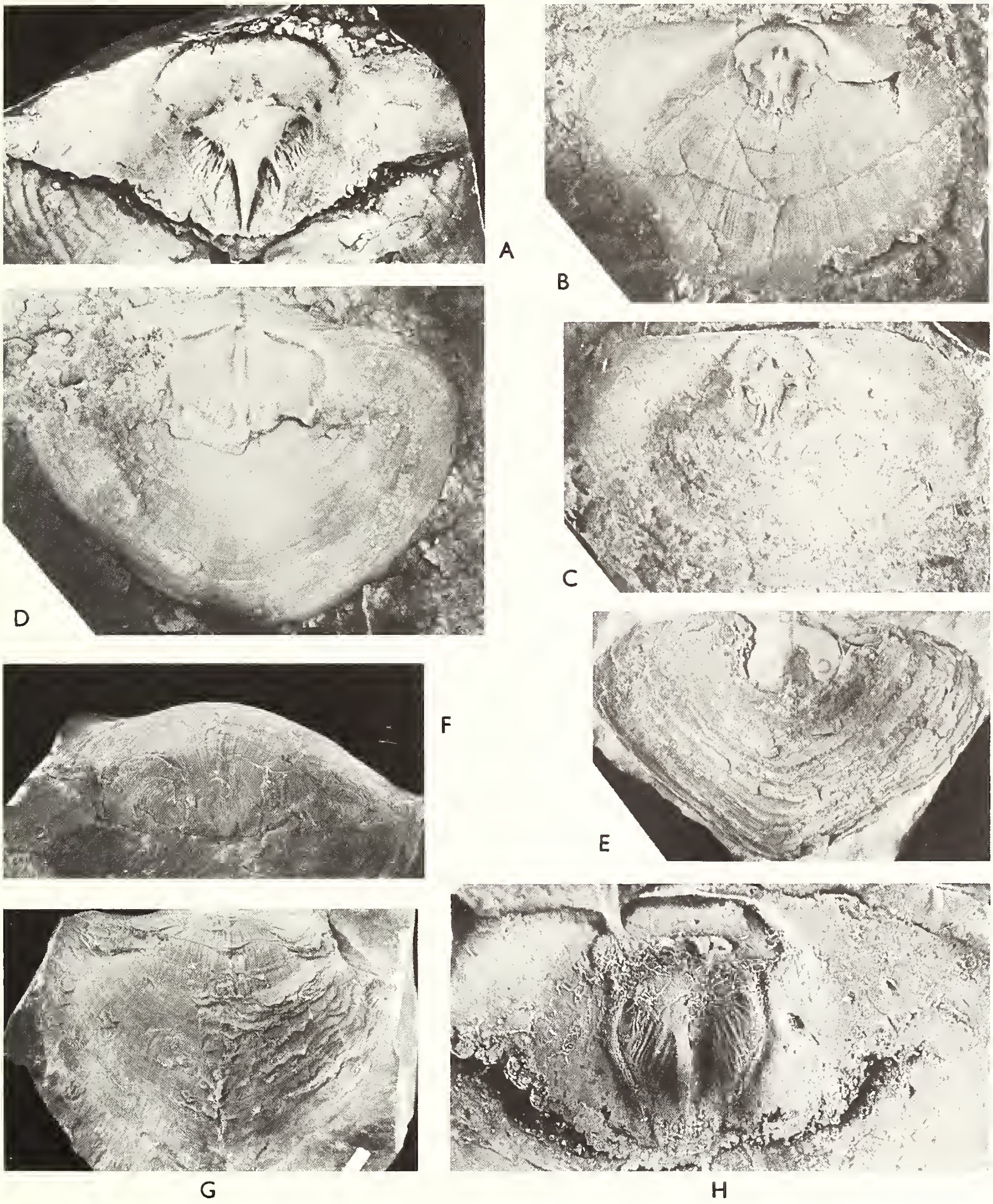
Material. Fifteen conjoined pairs, 12 pedicle valves, and 23 brachial valves; much of the material is represented by either broken or fragmentary valves.

Holotype. A pedicle valve, PMO 13091.

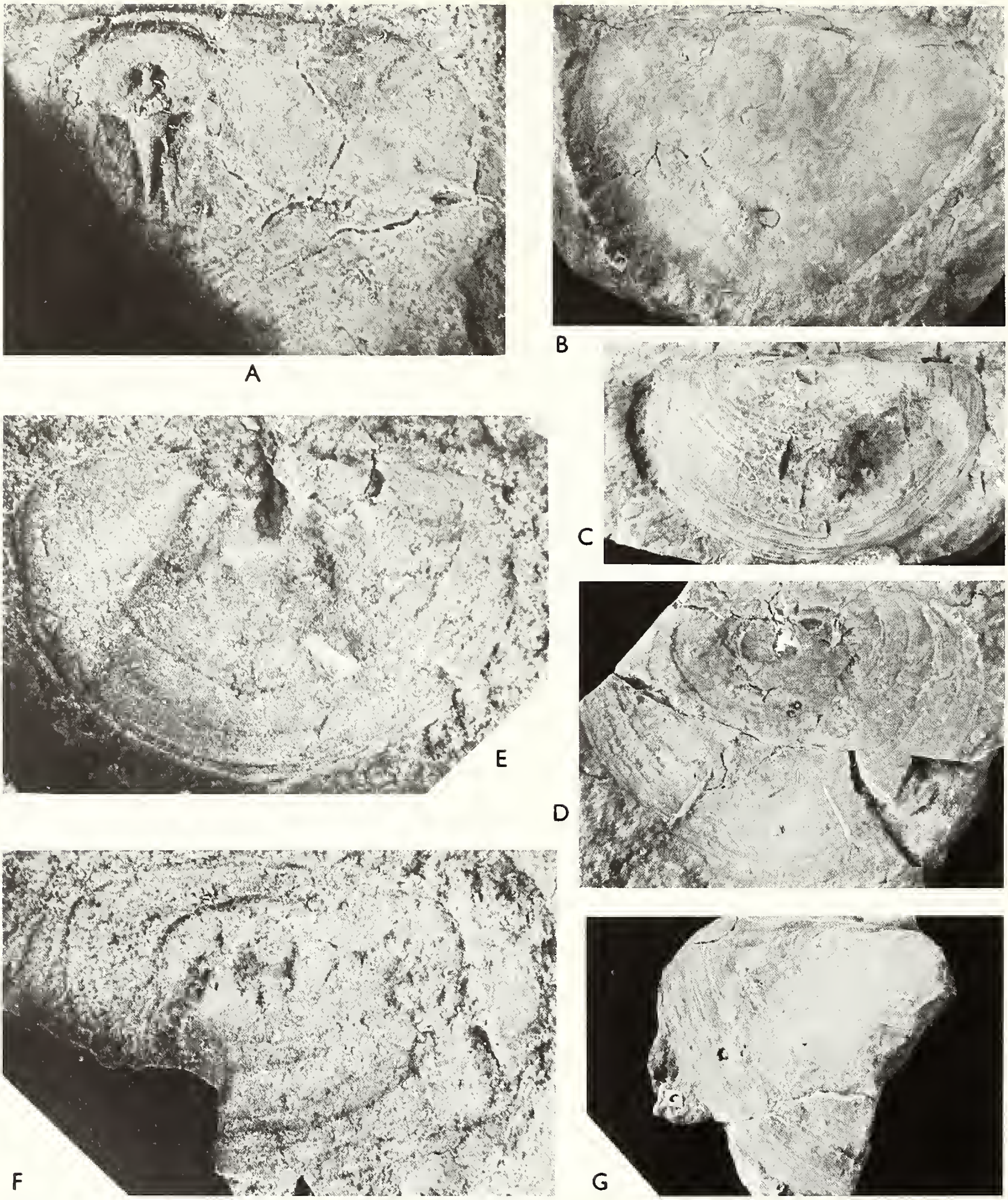
Diagnosis. An elongate *Gasconsia* with about 9–10 ribs per 10 mm at the 30 mm growth stage and about 3–4 thickened concentric growth lines per 10 mm at a similar place.

Description.

Exterior. Very large, thick, convexiplane to convexiconcave valves of elongate, rounded triangular outline with maximum width at or near mid-valve length; cardinal extremities obtuse and curved. Pedicle valve roughly flat or weakly concave in both anterior and lateral profiles, about three-quarters as long as wide. Well-defined but relatively short apsacline pseudointerarea about one-eighth as long as wide and about one-tenth sagittal valve length. Interarea modified by differentially thickened, transverse growth lines and narrow depressed homeodeltidium; latter occupies about one-fortieth width of interarea. Brachial valve about four-fifths as long as wide and about one-quarter as



TEXT-FIG. 3. A–H, *Gasconsia worsleyi* sp. nov., upper part of the Bønsnes Formation (Rawtheyan), Stamnestangen. A, silicone rubber replica of internal mould of brachial valve, PMO 104.000, × 1. B, dorsal interior, PMO 13831, × 2. C, silicone rubber replica of internal mould of brachial valve, PMO 103.999, × 1. D, holotype, ventral interior, PMO 13091, × 1. E, partly exfoliated ventral exterior, PMO S2275, × 0·5. F, G, posterior and dorsal views of dorsal exterior, PMO 17558, × 0·4. H, silicone rubber replica of internal mould of brachial valve, PMO 104.002, × 1·33.



TEXT-FIG. 4. A, *Gasconsia worsleyi* sp. nov., upper part of the Bønsnes Formation (Rawtheyan), Stamnestangen, silicone rubber replica of internal mould of brachial valve, PMO 104.001, ×2. B–G, *Gasconsia schucherti* Northrop, Gascons and Bouleaux formations (upper Silurian), Gaspé peninsula. B, lectotype, internal mould of pedicle valve, YPM 13313A, figured Northrop 1939, pl. 12, fig. 8; ×0·5. C, internal mould of brachial valve, YPM 13312, figured Northrop 1939, pl. 13, fig. 7; ×1·33. D, external mould of brachial valve, YPM 13313B, figured Northrop 1939, pl. 12, fig. 7; ×0·66. E, dorsal interior, YPM 13897; ×1·5. F, dorsal interior, YPM 13898; ×1·33. G, internal mould of brachial valve, YPM 13311; ×0·66, figured Northrop 1949, pl. 12, fig. 6. Figs. B, E, F are of specimens from the Bouleaux Formation (west side of Pointe Bouleaux Anse-A-la-Barbe, Gascons), the other figured specimens are from the Gascons Formation (locality 23 of Northrop 1939).

All specimens were whitened with ammonium chloride sublimate prior to photography; figs. E and F were photographed with a high-contrast film to enhance detail.

deep as long. Anterior profile strongly curved with maximum convexity medianly; flanks weakly concave, particularly near valve margins. Lateral profile strongly convex over posterior third of valve surface, anteriorly more evenly curved. Pseudointerarea short, virtually obsolete. Ornament of differentially thickened growth lines locally developed as rugae and over the anterior shell surface appearing as comae; 3–4 per 10 mm are present medianly at 30 mm growth stage. Rounded fine costae and costellae apparently restricted to inner shell surfaces number 9–10 per 10 mm medianly at 30 mm growth stage.

Ventral interior. Transverse semielliptical solid platform (text-fig. 2A) about two-thirds as long as wide and extending anteriorly to about two-fifths valve length. Platform delimited posteriorly by low, curved ventral plate rising vertically from floor of valve, lateral parts of which diverge widely anteriorly to near one-sixth valve length where they converge to describe evenly rounded curve. Large pair of anterior scars about three-fifths as long as wide, situated centrally on platform and divided medianly by low broad ridge, itself flanked by two deep grooves; anterior parts of muscle tracks deeply impressed. Lateral scars elongate and confined laterally by ventral plate; posterior scars transverse, partly attached to ventral plate.

Dorsal interior. Well-defined solid platform (text-fig. 2B) consisting of two parts. Curved dorsal socket marks posterior margin of rounded transverse and slightly convex rectangle bearing pair of small but deeply impressed central muscle scars and larger transverse posterior muscle scars. Anterior part of platform elongately triangular and marked laterally by deeply impressed anterior muscle scars, with numerous anterolaterally directed ridges. Lateral scars, relatively small, inserted on anterolateral edges of posterior part of platform.

Remarks. As previously noted the valves of *G. schucherti* are more transverse than those of *G. worsleyi* and moreover both the radial and concentric ornaments of the type species appear finer than those of the Norwegian form. However the lack of detailed information regarding the interiors of the type species prevents a comparison of the internal features of both species.

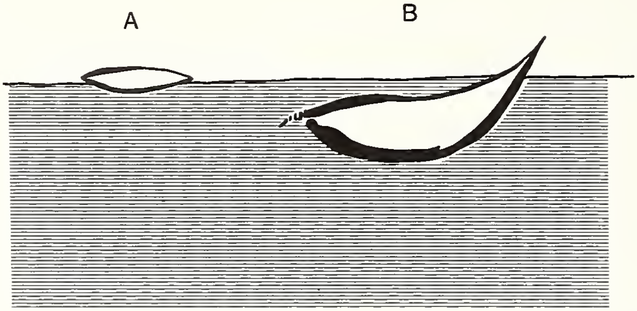
FUNCTIONAL MORPHOLOGY

Articulation of the valves of *Gasconsia* was achieved by the snug fit of the curved ventral plate into the dorsal socket. The muscles represented by the anterior and lateral scars when contracted would tightly close the two valves. The posterior muscles may also have contracted to supplement those adductors. Norford and Steele (1969, p. 164) suggested that to open the valves of the related trimerellid *Eodinobolus* Rowell muscles in the posterior part of the shells acted as diductors on contraction and therefore opened the valves about an axis delimited by the lateral edges of the interarea. This mechanism, however, is not feasible for *Gasconsia* as there is no area for muscle attachment behind the plate and socket whilst the function of muscles as diductors anterior to these structures is not possible. However, following the models of Gutmann *et al.* (1978) some of the muscles may have extended longitudinally from the posterior floor of one or both of the valves to attach directly to the coelom. Their contraction would have withdrawn the brachiopod animal posteriorly thus slightly forcing apart the shells. The central muscle scars of the lower brachial valve of *Gasconsia* do not appear to have counterparts in the pedicle valve. These scars may mark the site of attachment of such muscles; their contraction would have pulled the body posteriorly. Since lateral expansion of the body would have been inhibited by the lateral muscles, a dorsoventral distension of the animal's coelom would have raised the markedly lighter pedicle valve.

ONTOGENY AND AUTECOLOGY

Study of growth lines in different sized specimens of *Gasconsia* has permitted the reconstruction of the different growth stages of the shell during ontogeny. There is a distinct change in the type of growth between specimens less than 30–35 mm in length and larger ones. Specimens less than 30–35 mm in length have a gently convex brachial valve. In larger specimens, however, there is a sudden change from gently to strongly concavoconvex, reflected in a sharp change in convexity of the brachial valve. These changes in relative growth rates of the different parts of the shells are also combined with the development of great differential thickening of the brachial valve and the posterior part of the pedicle valve. This would have stabilized the shell against overturning, and the heavy posterior part of the shell may have partly sunk into the soft sediment.

The development observed in *Gasconsia* probably reflects different modes of life of young and adult individuals. Specimens less than 30–35 mm in length probably rested freely on the soft bottom with a more or less horizontal orientation of the commissural plane. The greater convexity of the brachial valve in larger specimens could be interpreted as an adaptation to a static, quasi-infaunal position (text-fig. 5). If sediment settled on to the concave pedicle valve, the shell may have been concealed except for the crescentic valve edges projecting above the surface of the sediment. This reconstruction of a quasi-infaunal position is very much like the presumed mode of life of many strophomenids, for example the productacean *Waagenoconcha* Chao (Grant 1966) from the Permian (see also Rudwick 1970, pp. 91–94).

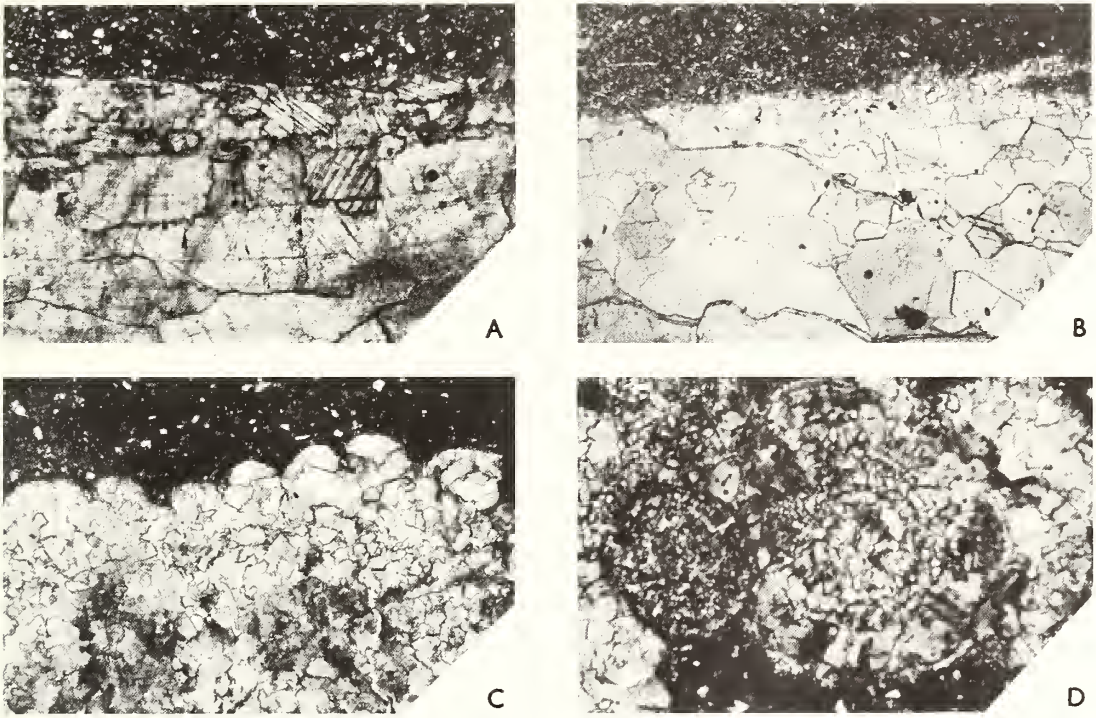


TEXT-FIG. 5. Reconstruction of life positions of young (A) and adult (B) specimens of *G. worsleyi* sp. nov. Young individuals probably lay on the sea floor while adults may have adopted a 'quasi-infaunal' mode of life. Both are sections through the median plane, the larger 75 mm in length, the smaller 30 mm.

Recent collecting at Stamnestangen has revealed a large conjoined pair of valves in a supposed life position. The orientation of the shells is consistent with the expected stable attitude of *Gasconsia* discussed above permitting the efficient opening and closing of the valves. The heavy umbonal region of the brachial valve was clearly anchored in the sediment whilst the markedly lighter pedicle valve could open freely.

SHELL STRUCTURE

Whilst the shells of the articulate brachiopods from the *Gasconsia* beds appear to display an original structure of fibres and lamellae of calcite (see e.g. Williams 1968*a*) the shell texture of the associated *Gasconsia* is strikingly different. (No shell material is available of the type species, *G. schucherti.*) The shells of *Gasconsia* are multilayered consisting of two intermixed phases (text-fig. 6A, B). The most prominent layers consist of a mosaic of sparry calcite; these are separated by thin indistinct zones, preserved as a diffuse linear arrangement of inclusions. These inclusions either cut the calcite mosaic, continuing without deviation across the intercrystalline boundaries, or separate the spar crystals in succeeding layers of sparry calcite. A similar microstructure has also been observed in gastropods and cephalopods from the same beds. Such a crystal fabric is evidence of an original aragonite shell diagenetically replaced by calcite with the retention of relict of 'ghost' texture (Bøggild 1930; Bathurst 1964). This supports the view of Jaanusson (1966) that trimerellid inarticulate brachiopods possessed the ability to secrete aragonite. Webby and Percival (1983, fig. 9B, E) have recently illustrated a similar secondary calcite fabric in shells of *Eodinobolus* from the Ordovician of New South Wales.



TEXT-FIG. 6. Photomicrographs of shell fabric of *G. worsleyi* sp. nov. A, part of shell, polarized light, ×25; the laminar relict shell structure is clearly visible whilst the grain boundaries of the secondary sparry calcite are less obvious. The shell-sediment interface is located near the top of the section. B, adjacent part of shell under cathodoluminescence, ×25; grain boundaries of secondary calcite are distinct whilst compactional fractures post-dating the calcite cement are pronounced. C, posterior part of shell showing development of warts, polarized light, ×25. D, detail of warts, polarized light, ×100; concentric primary structure clearly visible.

The inclusions, which represent traces of an original layered structure, indicate that the shells consisted of a number of sheet-like laminae orientated slightly oblique to the inner and outer shell surfaces (text-fig. 4A, B). Due to this oblique orientation the different laminae become exposed at the shell surface different distances from the umbo. The termination of these laminae at the outer surface are seen as growth lines. The most prominent and well-defined growth lines are composed of a series of thinner laminae whilst the more obscure lines consist only of a single lamina. In most cases the anterior termination of each lamina is separated from the shell surface and deflected outwards giving a characteristic serrated pattern in transverse section. This 'ghosted' original structure of *Gasconsia* is consistent with the well-established models of shell generation for the articulate brachiopods (e.g. Williams 1956, 1968*b*). The inversion to calcite prohibits speculation concerning the precise configuration and identity of individual lamellae. However since traces of an original fabric are locally preserved a form of replacement must have occurred rather than complete dissolution and recrystallization.

The shell interiors, particularly the posterior parts, are characterized by small rounded wart-like structures (text-fig. 6C, D). These are solitary or occur in irregular groups, and have sometimes grown along irregular lines making a complicated network (text-fig. 6C). There is a relationship between age and the number of warts in a shell with a general tendency for large shells to have a higher density than smaller ones. However the distribution pattern varies highly from individual to individual. In large specimens warts from the juvenile part of the shell are commonly completely engulfed by younger growth laminae, indicating that they ceased growing after some time. The warts vary in size, but most are about 0.5 mm in diameter. They are roughly hemispherical with growth laminae corresponding to the outer surface. The exact number of laminae in a wart is often difficult to discern due to replacement by sparry calcite, but in some well-preserved specimens more than twenty laminae could be counted. The distance between each lamina is about 0.08 mm. Although the warts may be explained as a response to some irritation which encouraged the brachiopod to secrete extra layers of aragonite there is no direct evidence for this view. Thin sections have not revealed any sign of associated foreign objects or borings. This may be preservational but more probably the irritant was organic and has since decomposed.

The shells have been extensively broken during compaction, but the resulting fractures are only visible in cathodoluminescence (text-fig. 6B). Since the now separated fragments of shell if reunited form a continuous crystal lattice, replacement of the original shell fabric occurred before breaking.

FAUNA AND DEPOSITIONAL ENVIRONMENT

Reconstruction of the depositional environment based on only one geological section is hazardous. In this case where lateral facies relationships are yet to be established in detail only a generalized picture of the depositional environment can be given.

In the Stamnestangen section the outcrop of the *Gasconsia* bearing beds is limited to a sequence about 20 m thick in the upper part of the Bønsnes Formation. *Gasconsia* is found as disarticulated or, less commonly, articulated shells in a microsparitic matrix. The associated fauna is characterized by a low species diversity (Table 1), in contrast to the rich shelly assemblages at the top of the Bønsnes Formation. The fauna is well-preserved, and except for tiny algal fragments, there is no sign of significant predepositional mechanical breakage or abrasion of skeletal material. The fauna and the fine-grained sediment indicate deposition in a rather constant low-energy environment influenced only by occasional stronger currents washing together skeletal fragments in thin horizons.

TABLE 1. List of associated species from the *Gasconsia* beds, Bønsnes Formation, Stamnestangen, Ringerike.

Articulate brachiopods	Sparse, minute dalmanellids, *Triplesia* sp., *Eospirigerina* sp. (all individuals minute).
Gastropods	*Maclurites* sp., *Murchisonia* (*Hormotoma*) sp., *Loxonema* (?) sp., *Lophospira* (?) sp., pleurotomariacean indet., holopeid spp.
Tabulate corals	*Palaeofavosites schmidti*, *P.* cf. *balticus*, *Catenipora tapaensis*, *Proheliolites dubius*, *Sarcinula organum*.
Rugose corals	*Streptelasma eccentricum*, *S. primum*, *S.* cf. *primum*, *Grewinkia anquinea*, *Bodophyllum eitlum*.
Calcareous algae	*Vermiporella* sp., *Dasyporella* sp.
Trilobites	Illaenid indet.
Trace fossils	*Planolites* sp., *Chondrites* sp.
Ostracods	Not determined.
Crinoid ossicles	Not determined.
Bryozoan	*Hallopora* cf. *multipora*.

As shown by Kiær (1920) calcareous algae are very common in this part of the sequence, especially fragments of *Vermiporella*; in some horizons these fragments constitute more than 90% of the skeletal debris. The presence of algae throughout the profile suggests that deposition took place within the photic zone. The present-day distribution of living calcareous codiaceans provides a good basis for interpreting the environmental regimes of similar fossil forms. Most modern forms colonize sand and mud substrates where the rhizoids of the plant penetrate the soft bottom to develop holdfasts (Wray 1977). Because of the delicate construction of these plants they generally live below intense wave agitation and are most common and diverse at depths of a few metres, especially in tropical shelf and lagoonal environments. It is generally inferred that most fossil species also had similar distribution.

The Bønsnes Formation is also well known for the great abundance of gastropods; in the older literature the term 'Gastropod Limestone' was often used for these beds. Parts of this fauna have been described by Koken (1925). Little is known about the palaeoecology of these Lower Palaeozoic gastropods, but according to Dr. J. Peel (pers. comm. 1982) the assemblage is suggestive of an algal browsing, or at least quiet water filtration existence.

The tabulate corals are mostly found in growth position scattered throughout the sequence. Their stratigraphical ranges are not well known from the Oslo Region excepting the family Heliolitidae which was described by Kiær (1899, 1903). However, all these corals are also known from Estonia where they indicate an Ashgill age (Vormi and Pirgu stages; Dr. E. Klaamann, pers. comm. 1982). The solitary rugose coral fauna is fairly restricted comprising species which are all well known from the upper Ordovician of the Oslo Region (Neuman 1969). The corals have a ceratoid to trochoid shape except *Streptelasma primum* which is cylindrical. Specimens of *S. primum* commonly show sharp geniculations indicating a sudden change in growth direction. This is probably in response to being tipped over during stormy episodes, accompanied by rapid growth to re-orientate the calyx permitting continued feeding. A similar growth habit is also known for the Carboniferous coral *Caninia* sp. (Hubbard 1966).

The matrix is heavily bioturbated indicating aerobic bottom conditions throughout the sequence. The trace fossil fauna comprises at least three different species, but due to poor preservation only *Chondrites* sp. and *Planolites* sp. have been identified.

The evidence of the associated biota and lithofacies indicates that *Gasconsia* dwelt on or partly within a carbonate mud substrate in a shallow, warm, marine environment; the habitat was restricted and perhaps even lagoonal.

Acknowledgements. We thank the following for their identifications of parts of the Norwegian fauna; K. Brood (bryozoans), E. Klaamann (tabulate corals), B. E. E. Neuman (rugose corals), A. W. Owen (trilobites), and J. S. Peel (gastropods). D. L. Bruton (Paleontologisk Museum, Oslo) and Mrs. J. Lawless (Peabody Museum, Yale University) permitted the loan of specimens in their care. V. Jaanusson provided valuable discussion and A. J. Rowell and A. W. Owen critically read the manuscript; Jenny Orr typed various drafts. Harper's contribution was completed during tenure of N.E.R.C. Research Award GR3/4471. We thank David Worsley for his constant encouragement.

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ZOOID AND COLONY GROWTH IN ENCRUSTING CHEILOSTOME BRYOZOANS

by SCOTT LIDGARD

ABSTRACT. An initial comparison of growth patterns of encrusting cheilostome bryozoans reveals that the ways by which zooids and colonies grow are often important determinants of the comparative success of different species and colony forms among different habitats. These patterns appear to have changed in a major evolutionary trend, increasing morphological and taxonomic diversity, and causing the appearance of more versatile and more highly integrated modes of growth through time. The growth of colonies in encrusting cheilostomes can be regarded in terms of different processes and geometries of zooid budding. I present here a model of growth based on bud expansion, partitioning, and position. The model permits reconstruction and comparison of different modes of growth in both living and fossil colonies.

SOLITARY and colonial animals grow in very different ways. In most solitary animals, individuals are physically separate and genetically different. In contrast, the units (zooids, polyps, etc.) of a colonial animal, whose structure and development are most comparable to solitary individuals, are all physically connected and have the same genotype. Bryozoan colonies can grow into many different forms by altering the direction and rate of zooid origination and growth, with some colonies even changing form during different stages of growth. Colonies of species with different patterns of zooid development often have the same overall form. It therefore seems reasonable to assume that bryozoan evolution involves changes in developmental patterns of both zooids and colonies. Little is known, however, of the extent to which these factors are interdependent.

Differences in the ways in which zooids and colonies grow are important not only in understanding the evolution of form, but also in understanding the ecology of species in different habitats. Moreover, these differences can be related to evolutionary changes in the distribution and abundance of taxa through time. Most bryozoans and other colonial animals are sessile, so movement to escape competition, predation, or injury is accomplished only by growth or, in successive generations, by larval dispersal. Consequently, the way a colony grows can profoundly affect how successfully it occupies space and competes for resources, or the likelihood of its surviving predation or injury (Jackson and Buss 1975; Buss 1979, 1980, 1981; Jackson 1979*a*, *b*, 1981, 1983; Jackson and Palumbi 1979; Jackson and Winston 1981). The appearance of new modes of growth in the fossil record apparently resulted in several major evolutionary trends in encrusting colony form, altering patterns of species richness and local abundance, and also apparently shifting the balance of competition among encrusting species by introducing new mechanisms for competitive overgrowth (Lidgard and Jackson 1982; Lidgard 1983; see also Jackson 1981 and references therein). The ecological structure of living faunas of encrusting cheilostomes is in many ways a culmination of successive evolutionary changes: a progressive trend towards increasingly varied and more versatile modes of growth.

Attempts to generalize about modes of colony growth have been characterized by a tendency to extrapolate from detailed studies of one or a few species. However, the cumulative diversity of modes of growth revealed by previous studies (e.g. Lutaud 1961, 1983; Schneider 1963; Banta 1968, 1969, 1970, 1971, 1972; Gordon 1971*a*, *b*; Hakansson 1973; Silen 1982; and others) has demonstrated the need for a more synthetic approach (Cheetham and Cook 1983).

Zooids within colonies form sequentially, preserving a morphological record of growth in both the zooid skeleton and that of the colony as a whole. This second record relates to an additional level of development not present in solitary animals, reflecting a pattern of overall growth of the colony as

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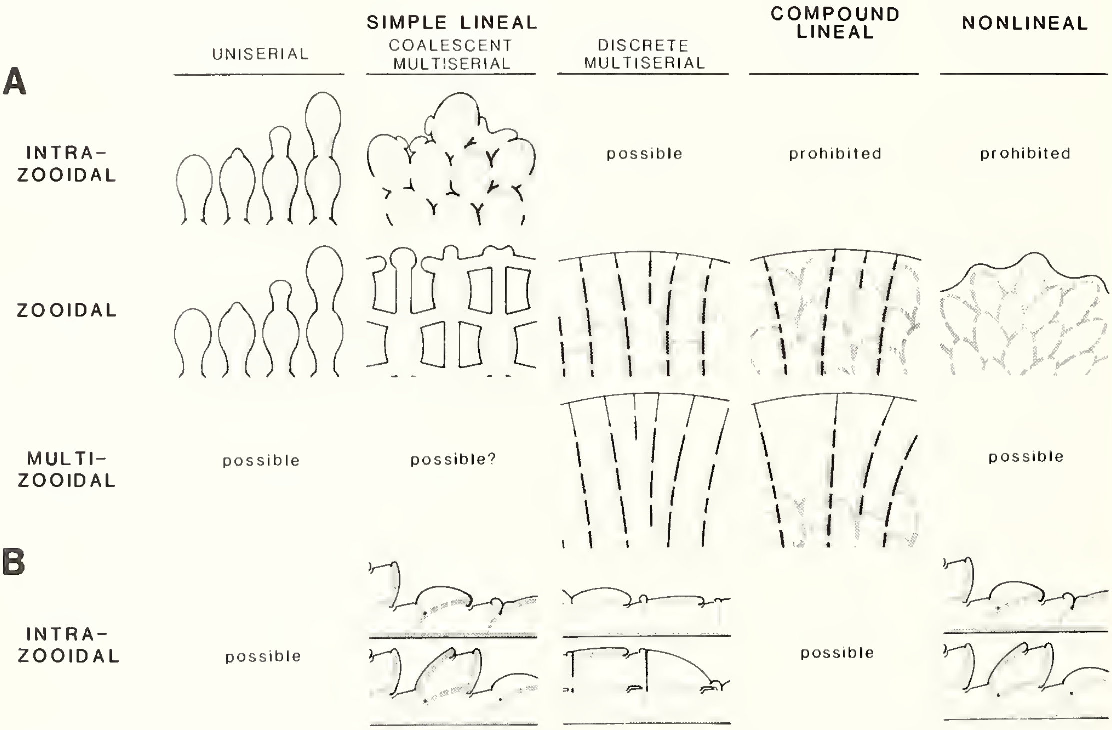
well as the ontogeny of individual zooids. Within a given colony a nearly complete sequence of zooid ontogeny can be reconstructed by comparing zooids at different stages of development. While growth of colonies is obviously linked to the formation of new zooids it may not be rigidly dependent on all aspects of zooid ontogeny. Colony development may actually exert some degree of control over zooid development, for example by determining the geometric arrangement of zooids or the rate at which successive ontogenetic stages are reached. This relationship between zooid and colony development has remained remarkably flexible throughout the history of cheilostomes.

In this paper I present a model of growth for encrusting cheilostomes (text-fig. 1). The model is primarily descriptive rather than predictive, being a means of reducing the inherent variability and morphological complexity of growth to relatively few elemental structures and processes. The model is a simple matrix of possible combinations of budding processes and geometries (Lidgard, in press). The different combinations do not represent individual species, but rather morphogenetic states that may occur singly or in combination within a single species or a single colony. For example, a given species may initially encrust a substrate by single-layered sheet-like growth, then develop a mound-like form by multilayered growth. Recognizing which combinations are shared by different taxa and which ones may be prohibited by structural, functional, or developmental constraints can only be accomplished empirically by determining boundary conditions from budding morphologies in a wide range of species, and not from *a priori* consideration of the patterns themselves (Boardman and



TEXT-FIG. 1. Growth model for encrusting cheilostome bryozoans based on patterns of zooid budding. Matrix rows represent budding processes; columns represent budding geometries. Combinations of process and geometry are morphogenetic states that may occur singly or in combination within a given species or colony. Known combinations are shown as idealized horizontal sections (in plan view) of zooids at the growing edges of colonies for (A) single layered growth; and as longitudinal sections for (B) multilayered growth. Exterior walls are shown with bounding cuticle (lines) and skeleton (stippled); interior walls with skeleton only.

Cheetham 1969). I first develop a framework for defining and comparing different budding processes and geometries, and extend this framework to include newly recognized modes of encrusting growth. I then consider how these modes of growth may be related morphologically, and finally how their evolution may be related to ecological patterns of occurrence and interaction of species, and to phylogenetic development within the major clades of cheilostome bryozoans through time.

MATERIALS AND METHODS

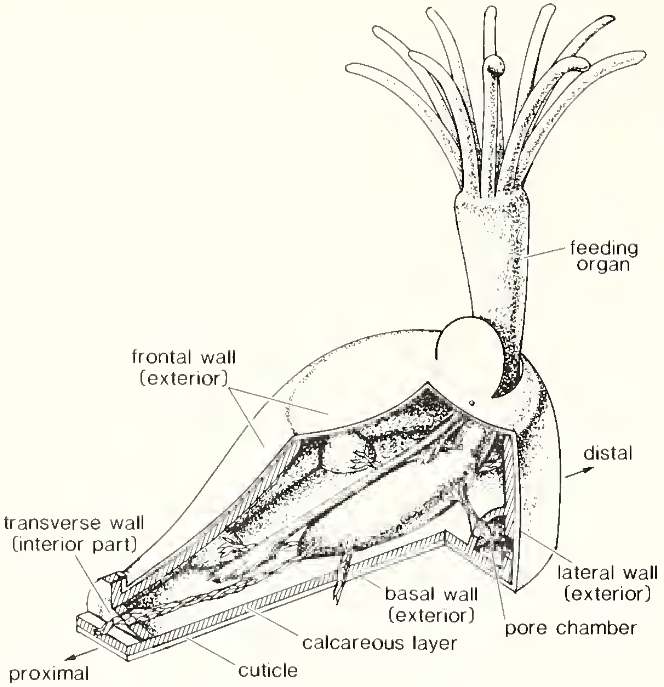
Budding patterns vary among cheilostome species, so any comprehensive study of growth must include a comparative survey of zooid and colony morphology. Many aspects of the model presented here resulted from a survey of more than three hundred fossil and Recent species in the collections of the United States National Museum of Natural History and in my own collections from the Atlantic Coastal Plain of North America. A preliminary model of budding patterns was derived from observations of whole-colony morphology, geometric arrangement of zooids, and the relative positions of zooid body walls and their apparent sequence of formation. Species were chosen to maximize the sample range of colony morphologies and higher taxa, and in some cases to duplicate previously described budding processes and geometries (Cheetham and Cook 1983, and references therein). Based on this survey a representative subset of species was selected for more intensive study using thin section and SEM techniques.

The advantages of epoxy resin embedding and thin sectioning to determine relationships of calcified and 'soft' tissue morphology *in situ* have been demonstrated in several recent studies of cheilostome growth (Banta 1968, 1969, 1970, 1971, 1972; Cook and Chimonides 1981*a*; Cheetham and Cook 1983; and others). In particular the developmental sequence of membranous, cuticular, and calcified zooid body walls can be inferred from sections cut through zooids and zooid buds at growing edges, or through zones of frontal budding from the surface of a colony. These, in turn, may be used to infer developmental sequences in analogous skeletal structures in fossil material. Thin sections of living colonies were prepared by embedding in epoxy resin (Reichhold epotuf 37-128 with hardener 37-614) under vacuum following the method of Nye *et al.* (1972). Sections were then cut, polished, attached to microscope slides, and stained with crystal violet to increase contrast of tissues. While this procedure allows detailed comparison of 'hard' and 'soft' tissue growth it has the disadvantage of being confined to a two-dimensional plane. Complex spatial relationships of three-dimensional morphologies may be obscured by section orientation. In addition, some aspects of body wall morphology, such as the extent of cuticular layers in calcified walls, require magnification beyond the normal range of light microscopy (Sandberg 1983).

In order to circumvent these problems I developed a technique for preparation of three-dimensional internal sections of colony skeletal fragments suitable for scanning electron microscopy. Specimens were treated with sodium hypochlorite, rinsed, air-dried, and placed in small glass vials partially filled with filtered canada balsam. The vials were heated to lower the viscosity of the balsam prior to embedding under vacuum. Parts of the specimens and the balsam were then removed by grinding on a medium grit carborundum wheel, followed by flat surface sanding on fine grit carborundum paper. The glass vials reduced crazing and edge fracture in the brittle embedding medium. The prepared surfaces were then given a final high polish using an 1800 grit tin oxide slurry on a polishing wheel. The exposed edges of skeleton were etched for 20 seconds in 0·5% formic acid to reveal fine skeletal structure and enhance the relief of non-calcified cuticle in the body walls. The balsam embedding medium was then removed by heating and transfer of each specimen through several xylene baths. Trial and error with various drying techniques revealed that a final acetone bath prior to critical point drying (Denton DCP-1) of the specimens significantly reduced meniscus formation and structural distortion at skeletal grain boundaries. Specimens were then coated with gold-palladium and photographed in the SEM (Cambridge S4 Stereoscan). Unless otherwise noted, figured specimens are SEM photographs prepared by the above method. Specimens with USNM catalogue numbers are deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

THE ELEMENTS OF ZOOID BUDDING

Consider the bryozoan colony as a system of interconnected zooids joined to one another by their walls. In addition to body walls and enclosed body cavities the zooids include feeding organs and other organ systems essential to the functioning of the colony (text-fig. 2). Polymorphic zooids such as avicularia and kenozooids generally lack feeding organs and therefore depend on connections with feeding zooids for nutrients. Conversely, feeding zooids may depend on polymorphs for other colony



TEXT-FIG. 2. Idealized anascan cheilostome zooid showing conventions of zooid orientation and body wall morphology related to budding. Exterior walls include cuticular or membranous external layer, inner cellular layer(s), and generally an intermediate skeletal layer, whereas interior walls generally include only skeletal and cellular layer(s) (inner cellular layers not shown). Figure modified from Cheetham and Cook (1983).

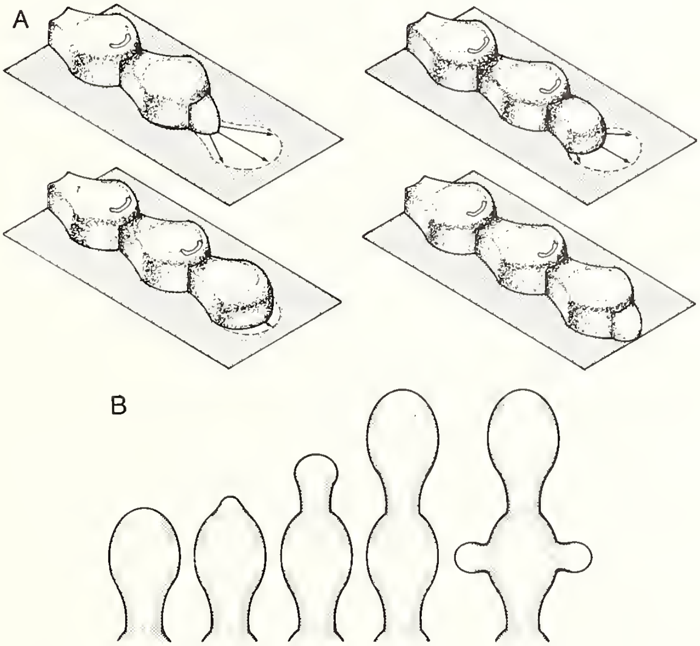
functions such as defence or structural support. Colonies gain new living space by asexually budding new zooids from pre-existing ones. A crucial element of this process is the formation of body walls that delimit zooids.

Cheilostomes have two distinct types of body walls (Silen 1944, 1982; Banta 1969; Cheetham and Cook 1983). *Exterior walls* extend the body of the zooid and the colony during growth. They are the boundary walls that actually or potentially separate the interior coelomic space and tissues of a colony from the environment. As they grow these walls include an outermost cuticular layer and inner cellular layers. In all but the simplest and morphologically primitive groups the principal exterior walls also include an intermediate calcified skeletal layer. *Interior walls* grow into body cavities of zooids or of multizooidal parts of the colony. Their growth partially or completely divides existing space. They are generally calcified and may or may not include a cuticular layer. However, no part of an interior wall is in contact with the external environment and therefore a cuticle in an interior wall cannot be an exterior cuticle.

Budding geometries. Buds originate from specific parts of parental zooids and also from specific parts of the colony as a whole. Consequently the geometric pattern of budding is unavoidably linked to potential budding sites on individual zooids as well as the spatial arrangement of surrounding zooids (Gordon and Hastings 1979). Budding sites on autozooids can be distinguished relative to the principal growth direction of the zooid (text-fig. 2). Buds originate from body walls situated laterally, frontally, or transversely to the proximal-distal growth axis of the parental zooid. Proximal budding is rare, apparently limited to repair of damaged zooids (Banta 1969) and early post-metamorphosis growth in a few species. Budding from the basal wall, which occurs in some erect and rooted cheilostomes, is precluded in most encrusting species by their close attachment to the substrate. Budding sites are further dependent on the placement of uncalcified windows in skeletal walls, and on structures such as areolae that are commonly associated with frontal budding (Pl. 26, fig. 5; see also below).

Budding sites relate more generally to colony geometry. An encrusting colony form reflects the arrangement of groups of zooids that depend on the substrate for support. The positions of new zooids are constrained by the arrangement of existing ones. *Single-layered growth* enables a colony to expand and occupy an area on a two-dimensional substrate, while *multilayered growth* permits expansion in the third dimension above the substrate in the area already occupied (text-fig. 1). Single-layered budding therefore generally occurs at the edge of a colony on or directly above the substrate. Buds form at the ends of runner-like strings of zooids or at the margins of sheet-like colonies where many zooids are connected laterally. Mound-like colonies are formed by multilayered frontal budding or by single-layered budding with repeated episodes of self-overgrowth.

Zooids in a cheilostome colony are typically arranged in *lineal series* (text-fig. 3A), reflecting the parent–daughter budding relationship of successive zooids (i.e. not sexual reproduction). It is important to note here the distinction between a lineal relationship, based on the immediate ancestry of individual zooids, and a linear one, which specifies only a spatial arrangement (e.g. linear rows of zooids) without regard to budding relationships. Within a lineal series the outermost cuticle and at least some parts of skeletal and cellular layers originate as multizooidal layers that are continuous from one zooid to the next (Cheetham and Cook 1983). Some of these layers are also continuous within a series from basal through lateral and frontal walls. As the body wall of a single-layered colony expands, a transverse interior wall begins to develop by infolding of the inner cellular layers of adjacent exterior walls. When the transverse wall is complete and the bud attains the form of a complete zooid the multizooidal layers of the body wall can be considered part of the new zooid. This developmental sequence is then repeated, successively adding new zooids to the distal end of the series.



TEXT-FIG. 3. A, idealized sequence of distal bud formation in an anascan cheilostome; successive zooids are arranged in a single lineal series (modified from Cheetham and Lorenz 1976). B, uniserial budding geometry shown as horizontal sections through zooids at the growing edge of a colony; budding sequence corresponds to A, while figure at far right illustrates the formation of lateral buds; interior and exterior body walls depicted as in text-fig. 1.

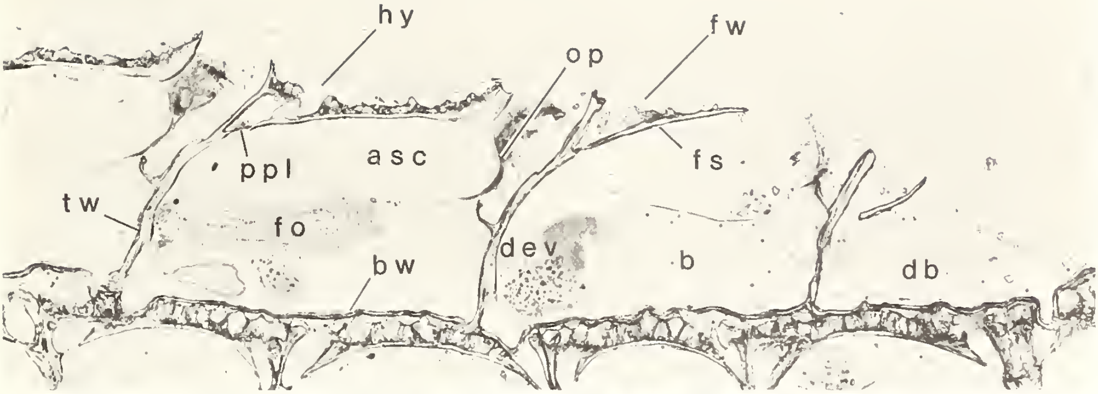
Budding processes. Budding involves two structural processes: expansion of the body cavity and enclosing walls beyond the existing limits of the parental zooid(s), and partitioning of this expanded region into one or more buds separate from the parental zooid(s). Each bud can be regarded as an early stage in zooid ontogeny, i.e. it will ordinarily develop into a functional zooid. It is therefore important to distinguish the space that will, in the normal course of development, become a new zooid (a bud) from the space that will remain part of a parental zooid.

Expansion begins as an outswelling by growth of cuticular and cellular layers of the parental zooid's exterior wall (Pl. 26, fig. 1; Lutaud 1961, 1983; Banta 1969; Tavener-Smith and Williams 1972), or of the multizooidal exterior wall of a budding zone adjacent to more than one parental zooid (Hakansson 1973). In calcified exterior walls, skeletal deposition generally begins in a zone of cell division proximal to the advancing edge of the bud. Expansion continues as the bud assumes the external morphology of a complete zooid.

An interior wall that partitions a bud from its parent may begin to develop before, during, or after bud expansion. Growth is initiated from the inner cellular layers of an exterior wall or, subsequently, from an existing interior wall. The new wall eventually grows into contact with the existing body walls, completely partitioning the original body cavity except for one or several uncalcified openings left during growth. These openings will become filled by communication organs composed of skeletal pore plates and 'special cells' (Banta 1969; Gordon 1975; Bobin 1977) that connect the funicular systems and body cavities of adjacent zooids. Communication organs are here termed *intraserial* when developed within a lineal series during distal or lateral budding (text-figs. 3, 4), or at the distal bifurcation of series (Pl. 26, fig. 2; text-fig. 5). They are formed as part of the normal growth of interior walls (Pl. 26, fig. 4). Adjacent series may also develop new communications laterally through *interserial* (between lineal series) communication organs (Pl. 26, fig. 3; see Silen 1944; Banta 1975; Banta and Wass 1979). The growing edges of adjacent series advance in unison, leaving matching uncalcified windows in their respective lateral walls. In these windows the double cuticle layer is dissolved, breaching the walls (Banta 1969). Simultaneously a small interior wall consisting primarily of a pore plate and cellular layers extends from the breached exterior wall into the more proximal of the two zooids. The completed wall will become part of a communication organ linking the adjacent zooids. While these two types of communication organs differ in their mode of formation, their function in completed zooids appears to be the same.

EXPLANATION OF PLATE 26

Figs. 1–5. *Metrarabdotos unguiculatum cookae* (Cheetham), Ghana, west Africa, Recent. 1, USNM 243229 (Cheetham and Cook 1983); 2–5, USNM 376699. 1, sequence of zooid development is apparent in succession of newly budded zooids at growing edge of a colony. Longitudinal thin section through a single lineal series illustrates concurrent development of body walls and other organ systems. Growing edge is encrusting another portion of the same colony. Calcified basal wall (bw), transverse walls (tw), and membranous frontal wall (fw) enclose zooid body cavities. Distal bud (db) at far right has no frontal shield, ascus, or feeding organ. Progressive development of these structures is shown in successively more proximal zooids. Areolae, which include communication organs with skeletal pore plates (ppl) that develop in the frontal shield, permit communication between the hypostegal coelom (hy) and principal body cavity (Banta 1972, 1973). Body walls, ascus (asc), operculum (op), and feeding organ (fo) are fully developed in zooid at left. Bubble (b) is an artifact of the embedding process, × 70. 2, frontal skeletal surface of colony growing edge; budding geometry is discrete multiserial; budding process is zooidal (note quincuncial arrangement of zooids and bifurcation of lineal series at centre), × 35. 3, side view of fig. 2 reveals internal skeletal morphology of lineal series, inter- and intraserial pore plates, and transverse walls that separate zooids within lineal series, × 35. 4, detail of interior transverse wall (tw) showing intraserial pore plates (ppl) and lack of cuticle, × 200. 5, detail of skeletal morphology of areola (ar) and pore plates (ppl) in frontal shield, × 275.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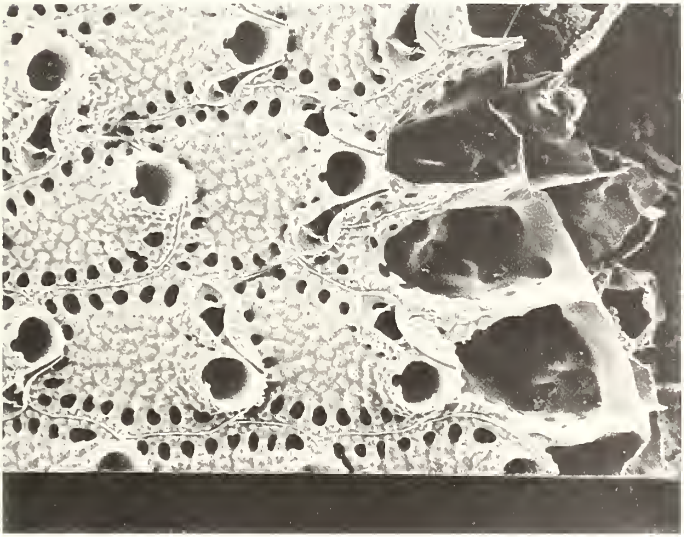

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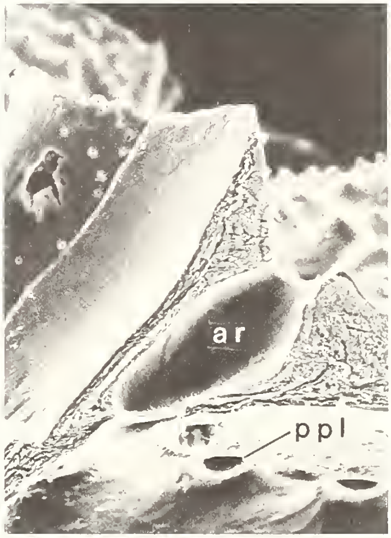

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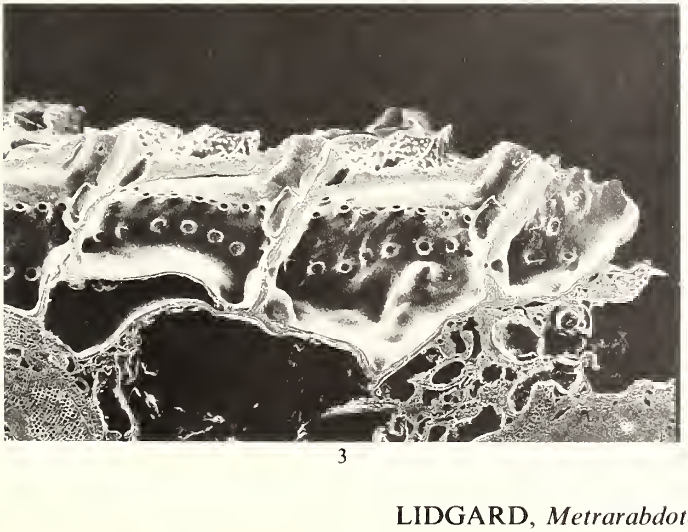

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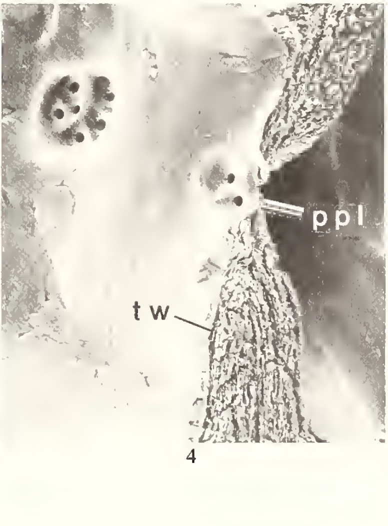

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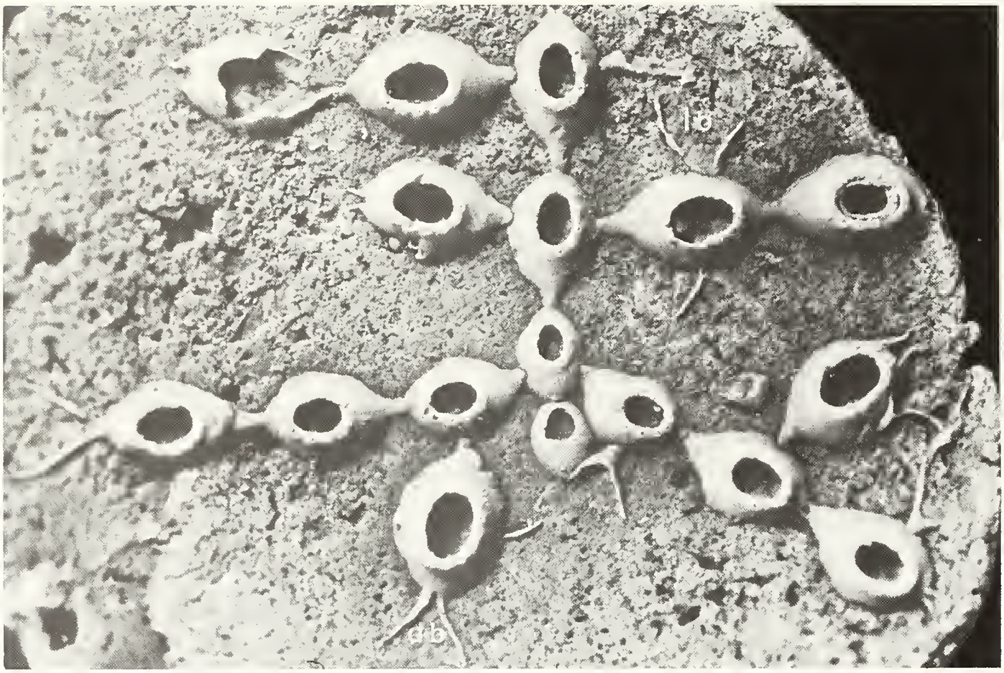
LIDGARD, *Metrarabdotos*



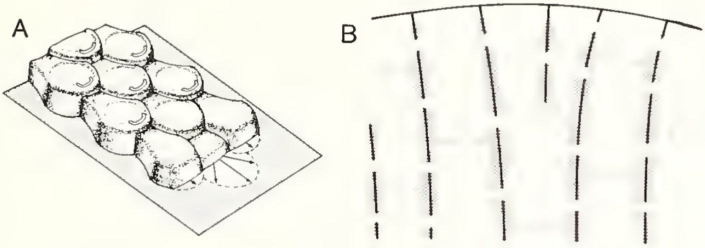
TEXT-FIG. 4. *Allantopora irregularis* (Gabb and Horn), USNM 242558, Noxontown Millpond, Delaware, Palaeocene. (Cheetham and Cook 1983), uniserial budding geometry showing both distally (db) and laterally (lb) budded zooids. Budding process is zooidal. Light photograph; specimen stained, coated with ammonium chloride, ×28.

The model presented here resolves morphology only to the coarsest level of body wall development. This implicitly assumes that post-larval developmental processes at other levels (i.e. cellular mechanisms of skeletal secretion, organogenesis, and others) are related to body wall development in a predictable way. While available evidence suggests that this is indeed the case (Tavener-Smith and Williams 1972; Sandberg 1983; Lutaud 1983, and references therein), development of feeding organs and most other intra- and extra-zooidal parts will not be considered here. Nor will I explicitly consider the budding of polymorphic zooids other than to note that the concepts of budding process and geometry presented here for the development of feeding zooids should apply to polymorphs as well.

SINGLE-LAYERED BUDDING

Geometries

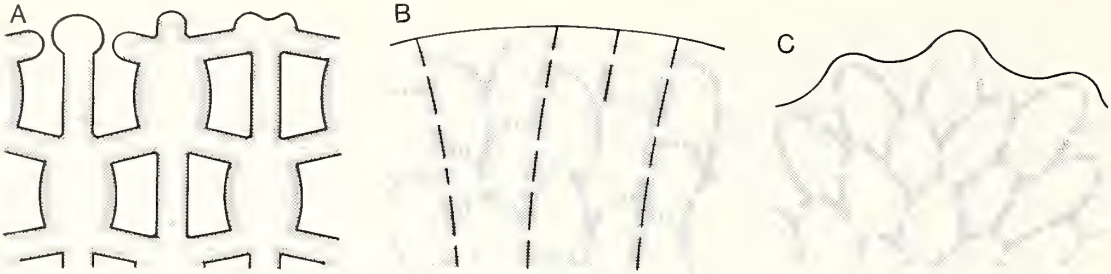
Simple lineal geometries. Colonies in which lineal series remain more or less separated from one another, forming a runner-like colony morphology, are termed *uniserial* (text-figs. 3, 4). In uniserial species such as *Pyripora catenularia* (Fleming), contacts between series are irregular, and interserial communication organs are rarely if ever developed (Banta 1975; but see also Gordon and Hastings 1979). Budding is not limited to the distal end of a series. New series may be initiated from laterally placed budding sites by the same developmental sequence as distal budding. The interior wall that partitions a parental zooid from a laterally positioned bud is formed without dissolution of exterior cuticle. Therefore the communication organs at this junction between series are intraserial rather than interserial (Silen 1944). However, only a fraction of lateral budding sites ever give rise to new lineal series. Lateral budding enables a uniserial colony to form new zooids in any region of the original series, even after the growing edge has advanced past the point of lateral bud formation. This ability can be recognized in fossil species by the presence of partially developed calcified walls in older regions of the colony (text-fig. 4) and is present even in the earliest uniserial colonies (Pohowsky 1973).



TEXT-FIG. 5. Discrete multiserial budding. A, idealized anascan colony showing distal bud formation in three adjacent lineal series (modified from Cheetham and Lorenz 1976). B, horizontal section through zooids at the growing edge of a colony; interior and exterior body walls depicted as in text-fig. 1; intra- and interserial communication organs shown as openings in body walls; note the bifurcation of lineal series at centre.

In *discrete multiserial* colonies, frequent or continuous contact of adjacent lineal series results in a sheet-like colony form (Pl. 26, fig. 2; text-fig. 5). Lineal series abut one another along a double wall of two exterior walls whose outermost cuticular layers face one another directly. In sheet-like colonies of *Membranipora*, *Cryptosula*, *Schizoporella*, and many other genera, distal budding occurs simultaneously in a number of lineal series. However, buds in adjacent series are rarely at the same developmental stage. This is due at least in part to the quincuncial arrangement of zooids typical of many multiserial colonies, wherein each zooid borders two distolateral and two proximolateral neighbours. Lateral budding is constrained by the adjacent series blocking potential budding sites, except where lineal series diverge sufficiently to allow intercalation of a new series. Laterally adjacent lineal series do, however, develop intraserial communication organs, the formation of which involves processes that have been compared to budding (Silen 1944; Banta 1969).

As a multiserial colony expands, new lineal series must be intercalated at the widening colony margin. The apparent bifurcation of lineal series is a normal aspect of simple lineal budding (Pl. 26, fig. 2; text-fig. 5B). A longitudinal division appears at the advancing distal margin of a lineal series, usually in a medial position (Lutaud 1983). A portion of the membranous exterior wall becomes stationary at this division as the rest of the wall expands distally. Subsequent growth past the resulting indentation yields two 'buds' that will eventually become mature zooids. Since the advancing exterior body wall remains continuous with the centred stationary portion, the lateral wall separating the two new zooids is a double wall complete with intercalary cuticle. The process is comparable to distal and lateral bud formation in uniserial colonies, while here the lateral bud is moved to a distolateral location. As in the case of uniserial budding, the communication organs of the partitioning interior transverse wall are intraserial (Pl. 26, fig. 4). Growth of the new buds may laterally displace adjacent lineal series due simply to the width of the additional new series. A quincuncial arrangement of zooids is generally maintained as the new zooids will typically grow to different lengths. In some species the width of the parental zooid may increase to accommodate series bifurcation.



TEXT-FIG. 6. A, coalescent multiserial budding; new zooids are formed at the growing edge by fusion of proximally and laterally adjacent buds. B, compound lineal budding; each lineal series is composed of two or more adjacent rows of zooids partitioned by both interior and exterior lateral walls. C, nonlineal budding; zooids are partitioned by interior vertical walls within a laterally confluent budding zone. All are horizontal sections of zooids at growing edges of colonies; interior and exterior body walls depicted as in text-fig. 1.

Coalescent multiserial budding results from the fusion of adjacent buds to form a single zooid (Pl. 27, fig. 1; text-fig. 6A). This geometry is well developed in species of *Beania* in which zooids are connected by tubular extensions of the exterior body walls. The buds develop from two or more parental zooids, expand and contact one another, then dissolve the cuticular body walls at their point of contact to produce a single confluent bud (Silen 1944; Cheetham and Cook 1983). Thus lineal series are constantly anastomosing. The resulting bud will either begin a new series or produce subsequent anastomosis. It is assumed that bud fusion occurs only when buds contact before calcification (Banta 1975).

Compound lineal geometry. This multiserial geometry superficially resembles simple lineal budding (Pl. 27, fig. 2; text-fig. 6B). It is commonly developed in *Parasmittina* and is the same as the 'multizooidal budding' described by Silen (1982) in *P. trispinosa* (Johnston). As the body wall expands distally it forms a bud, two or more zooids in width and bounded by exterior walls as in an ordinary lineal series. Interior walls then develop to partition the coelomic space and form a compound lineal series of two or more rows of zooids. Interior walls thus separate zooids laterally as well as transversely within the series.

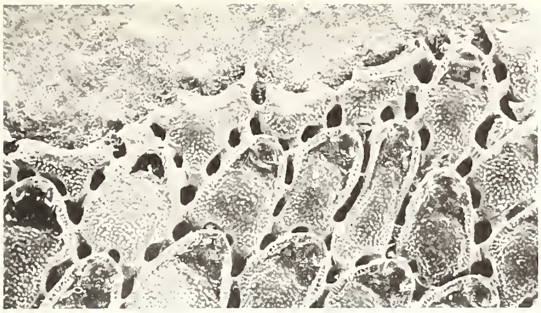
EXPLANATION OF PLATE 27

Fig. 1. *Beania simplex* (Heller), USNM 376700, Amalfi, Italy, Recent; frontal surface of colony with cuticle intact showing fusion of buds at colony margin; budding geometry is coalescent multiserial; budding process is zooidal, ×45.

Fig. 2. *Parasmittina nitida* (Verrill), USNM 376701, U.S. Fishing Comm. Sta. 5522, Vineyard Sound, Massachusetts, Recent; frontal skeletal surface of colony growing edge; budding geometry is compound lineal; budding process is multizooidal; light photograph of stained specimen coated with ammonium chloride, ×19.

Figs. 3, 4. *Cupuladria biporosa* (Canu and Bassler), USNM 376702, Nassau, Bahamas, Recent. 3, distal view of colony growing edge showing zooids at different stages of development; at left, basal wall (bw) is partially formed between laterally adjacent zooids; at right, bud with incomplete transverse wall (tw) prior to completion of pore plate, ×60. 4, frontal skeletal surface showing basal wall of bud at left in fig. 3; zooids are partitioned by interior vertical walls in a laterally confluent budding zone surrounded by membranous external cuticle (not shown); budding geometry is nonlineal; budding process is zooidal, ×70.

Figs. 5, 6. *Schizoporella floridana* (Osburn), USNM 376703, Pescaderabaai, Curacao, Recent. 5, frontal skeletal surface showing zooids in different lineal series at different stages of development, together with greatly elongated distal bud (cf. Pl. 26, figs. 2, 3); budding geometry is discrete multiserial; budding process is multizooidal, ×60. 6, side view of fig. 5, showing internal skeletal morphology of developing zooids, ×60.



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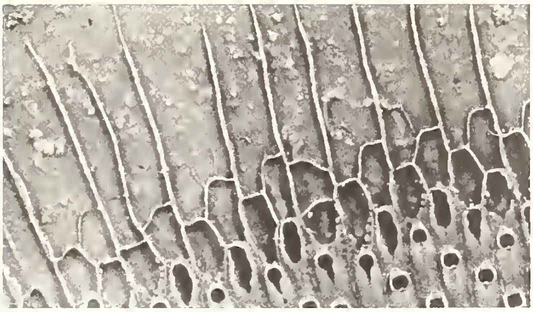

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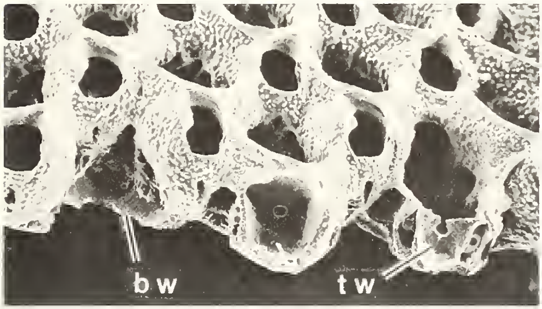

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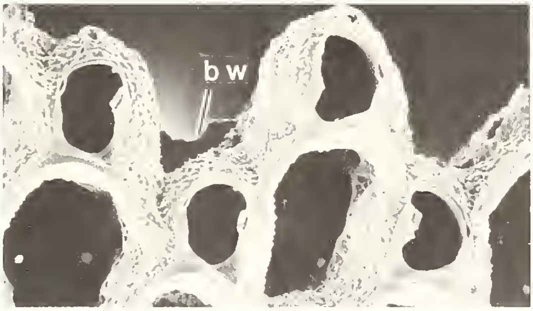

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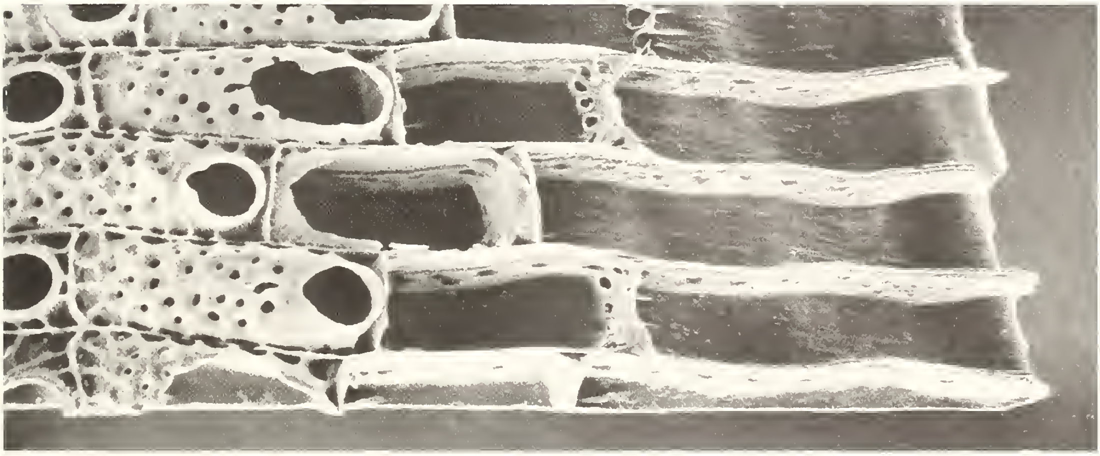

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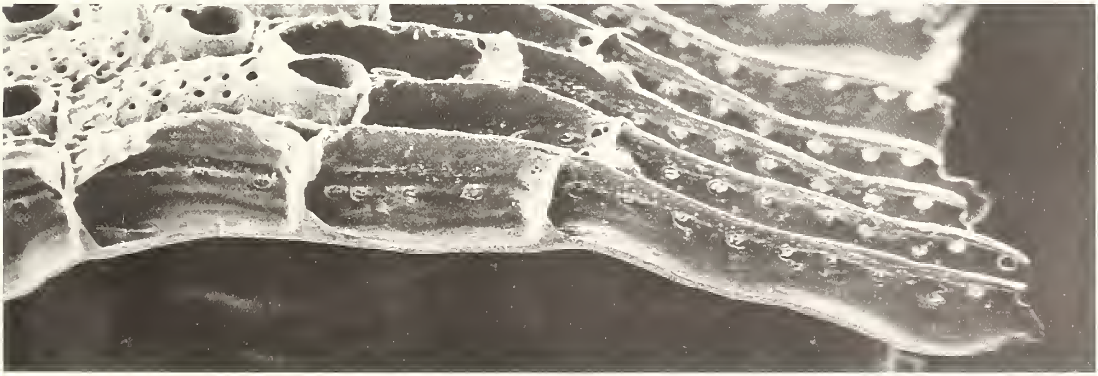


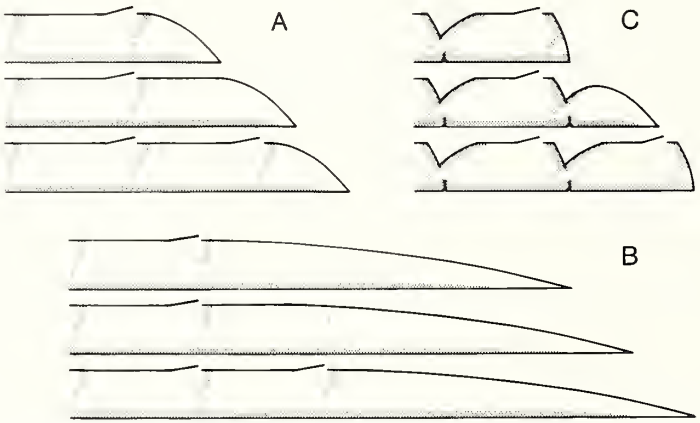
6

LIDGARD, *Beania*, *Parasmittina*, *Cupuladria*, *Schizoporella*

Within a compound lineal series, zooids are positioned in quincunx and apparently communicate entirely through intraserial communication organs in lateral and transverse interior walls. Laterally adjacent zooids in different compound lineal series communicate through interserial communication organs formed in the same way as those in simple lineal colonies. Because of observed similarities in the structure and geometry of the growing edge the process of bifurcation of lineal series can be inferred to be the same as that in simple lineal budding.

Nonlineal geometry. Confluent budding zones also exist in cheilostomes where lineal series are absent (Pl. 27, figs. 3, 4; text-fig. 6C). In the encrusting early stages of *Cupuladria*, new zooids arise in a budding zone that is laterally confluent around the entire colony margin (Hakansson 1973). Lineal relationships are obscure or non-existent, as new zooids within this zone are partitioned exclusively by interior vertical walls. During budding the exterior wall at the colony margin expands distally (and later basally, if the end of the substrate is reached). Buds arise on the colony margin not as separate units but rather as localized extensions of the confluent budding zone. During zooid formation a small area of uncalcified body wall begins to expand at the growing edge of the colony. Skeletal material is then deposited at the base of pre-existing zooid walls. Formation of the basal skeletal walls is continuous with deposition of interior lateral walls and, eventually, a transverse distal wall. The vertical walls are completed with the formation of communication organs (comparable in their mode of formation to intraserial communication organs; see below) between zooids. As the colony expands radially, new buds arise in the spaces between newly completed zooids, producing a quincuncial arrangement.

The usual transition from an encrusting to a free-living state in *Cupuladria* and similar forms is accomplished by expansion of the colony margin beyond the limits of the substrate. This transition is accompanied by basal expansion of the body wall and coelomic space to form extrazooidal structures that commonly complete the enclosure of the original substrate (Hakansson 1973, pl. 1).



TEXT-FIG. 7. Budding processes in single-layered growth. A, zooidal budding; zooids are partitioned by growth of interior wall proximal to the growing edge in a more or less continuous process. B, multizooidal budding; zooids formed as in zooidal budding, but buds are greater than two zooids in length. C, intrazooidal budding; zooids formed directly at the growing edge of the colony by a discontinuous process of bud expansion from pore chamber of parental zooid; note that pore chamber is completed prior to expansion of successive zooid bud. All are longitudinal sections of anascan zooids in lineal series showing different sequences of zooid formation at the growing edges of colonies; interior and exterior body walls depicted as in text-fig. 1.

Nonlineal budding is also regularly present in a number of free-living and loosely attached genera, some of which develop basal rootlets. In many species of *Selenaria*, *Conescharellina*, *Stichopora*, *Euthyrisella*, and others, zooids are partitioned by interior vertical walls in a laterally confluent budding zone enclosed by a membranous exterior cuticle (Cook and Chimonides 1981*a*, *b*; Hakansson pers. comm.). While colony form in these species differs significantly (and in many cases may not involve an extensive encrusting phase), the nonlineal budding process appears to be little different from that described for *Cupuladria*.

All vertical walls in *Cupuladria* and other species with nonlineal budding are interior walls, and hence communication organs do not breach exterior cuticle. However, use of the term intraserial to describe these communication organs is misleading since lineal relationships between zooids are obscure. Banta (1969) showed that the communication organs developed in exterior walls form a peripheral ring of cuticle (annulus) where the intermediate cuticle has been breached. Communication organs formed in interior walls lack this structure. The terms annular and nonannular were proposed to distinguish between these differences in morphology and development. I have not adopted these terms here because they lack the utility of intraserial and interserial in defining position and lineal relationship as well as developmental process in the majority of cheilostome species.

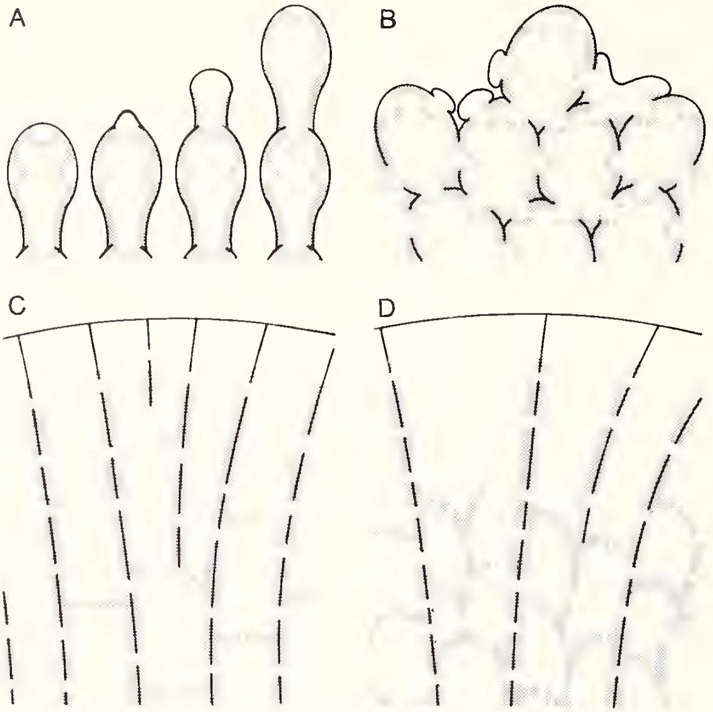
Processes

Zooidal budding. The relative timing of bud expansion and partitioning may also differ in single-layered growth. In genera such as *Aplousina*, *Cryptosula*, *Watersipora*, and *Smittoidea* the expanding bud generally extends beyond the distal margin of the parental zooid before or during the completion of its partitioning transverse wall (Pl. 26, figs. 1–3; text-fig. 7A). The transverse wall is shared by the newly formed zooid and the expanding bud that will form the next zooid. This process can be termed *zooidal*. Bud expansion appears to be a relatively continuous process, although the rate of growth may vary considerably with the condition of the colony or certain environmental factors. However, large changes in growth rate or even cessation of growth appear to be random with respect to the developmental stage of any given zooid (cf. Lutaud 1983). Zooidal budding is the dominant budding process among living cheilostomes. All of the budding geometries described in the previous section occur in species with zooidal budding.

Multizooidal budding. Buds that expand to two or more zooidal lengths before transverse walls begin to partition them are here termed *multizooidal* (Pl. 27, figs. 5, 6; text-fig. 7B) and are equivalent to giant buds described by Lutaud (1961, 1983; see also Cheetham and Cook 1983). Multizooidal and zooidal budding are end members of a continuum involving virtually the same continuous developmental process, but with striking differences in the timing of zooid ontogeny. Although some species such as *Membranipora membranacea* (Linnaeus), *Stylopoma spongites* (Pallas), and *Schizoporella floridana* (Osburn) commonly exhibit both budding processes, most species never develop multizooidal buds. Therefore, the potential for multizooidal budding can be regarded as a morphologically useful if somewhat arbitrary division.

Multizooidal budding is most commonly present in species having a simple lineal discrete multiserial budding geometry (text-fig. 8C). Most of these species also bud zooidally in some parts of the colony or during different stages of colony growth. Increased bud length in *M. membranacea* and other species is positively correlated with growth rate and colony size, and in some cases its expression may be dependent on environmental factors (Lutaud 1961, 1983; see also Edmundson and Ingram 1939; Menon 1972; Menon and Nair 1974; Mawatari 1975; Winston and Jackson, in press). Multizooidal budding is also present in some species of *Parasmittina* with compound lineal geometries (text-fig. 8D; Silen 1982). Multizooidal budding in uniserial and nonlineal geometries, though seemingly possible, is not known. Coalescence of multizooidal buds is rare or absent in most species with multiserial geometries, but may possibly occur when lineal series at the growing edges of a colony are constricted by an obstacle on the substrate (in most cases, lineal series simply terminate without coalescence). Multizooidally budding species that consistently employ a coalescent budding geometry (as in *Beania*) are not known.

Intrazooidal budding. In the majority of encrusting cheilostomes the partitioning body wall is completed during or after the expansion of a bud beyond the boundary wall of a parental zooid. However, as is apparent in colonies of *Microporella*, *Fenestrulina*, or *Cribrilina*, this is not always the case. *Intrazooidal* buds develop from a region within a parental zooid that will subsequently become part of a new zooid (Pl. 28, figs. 1, 2; text-fig. 7C). Before bud expansion begins this region is partitioned from the principal body cavity of the zooid by an interior wall containing intraserial



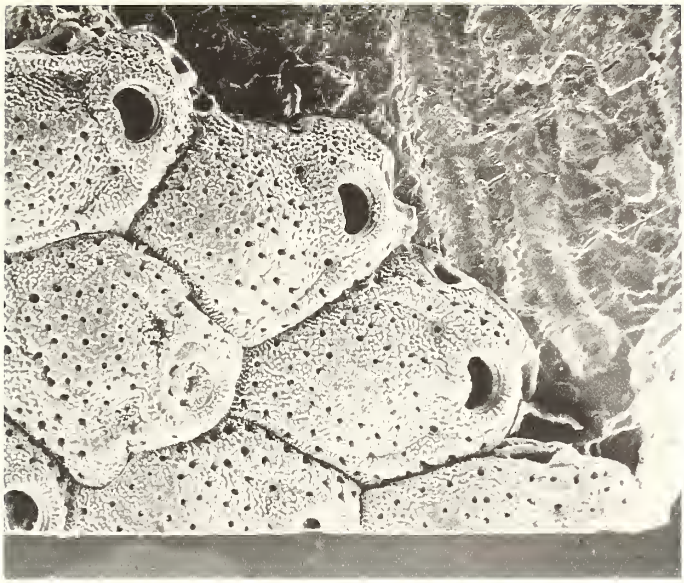
TEXT-FIG. 8. A, intrazooidal budding process with uniserial geometry; note pore chamber formation prior to bud expansion. B, intrazooidal budding process with multiserial geometry; both discrete multiserial and coalescent multiserial geometries (involving bud fusion) are often present in the same colony. C, multizooidal budding process with discrete multiserial geometry; buds are two or more zooids in length; new zooids are partitioned proximal to the growing edge. D, multizooidal budding process with compound lineal geometry; lineal series are composed of two or more rows of zooids partitioned by both interior and exterior lateral walls. All are horizontal sections of zooids at growing edges of colonies; interior and exterior body walls depicted as in text-fig. 1.

EXPLANATION OF PLATE 28

Figs. 1–4. *Monoporella nodulifera* (Hincks), USNM 376704, Albatross Sta. 2843, Unalaska, Alaska, Recent. 1, frontal skeletal surface showing predominance of fully developed zooids at the growing edge; budding geometry is discrete multiserial (although zooid at top centre may have formed by bud fusion and would therefore reflect coalescent multiserial geometry); budding process is intrazooidal, × 40. 2, side view of fig. 1, showing internal skeletal morphology including pore chambers (pch), × 40. 3, detail of distal bud showing calcified basal wall (bw) and remnants of cuticle insertion (cut) marking the distal extent of the parental zooid prior to bud expansion. Before a bud begins to expand the pore chamber (pch) is separated from the external environment by calcified external wall and an uncalcified window with a membranous exterior cuticle, × 125. 4, detail of pore chamber (pch) showing interior transverse wall (tw) with intraserial pore plates (ppl) and absence of exterior cuticle, × 230.

Fig. 5. *Pyriporopsis*(?) *texana* (Thomas and Larwood), USNM 242556 (Cheetham and Cook 1983), Fort Worth, Texas; Fort Worth Formation, Albian, Cretaceous. Frontal skeletal surface of colony showing uncalcified openings of distal and lateral pore chambers (pch); budding geometry is uniserial; budding process is intrazooidal; light photograph of stained specimen coated with ammonium chloride, × 45.

Fig. 6. *Wilbertopora mutabilis* (Cheetham), USNM 186568 (Boardman and Cheetham 1973); frontal skeletal surface of colony showing zooids in uniserial geometry succeeded by others in coalescent multiserial geometry; budding process is intrazooidal; light photograph of stained specimen coated with ammonium chloride, × 35.



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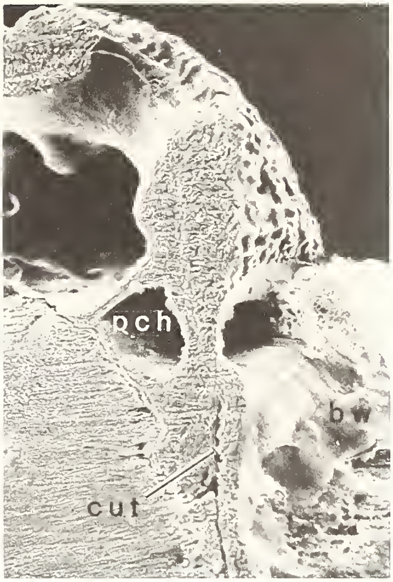

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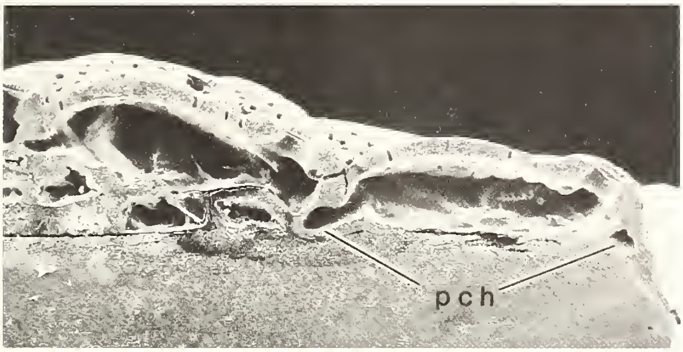

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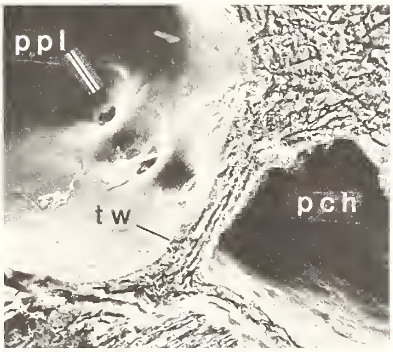

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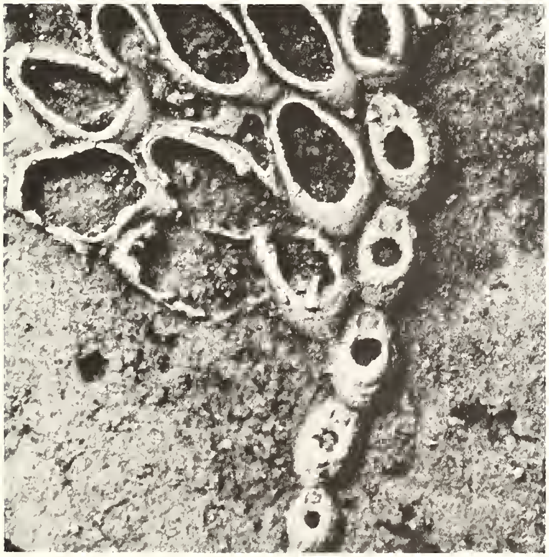

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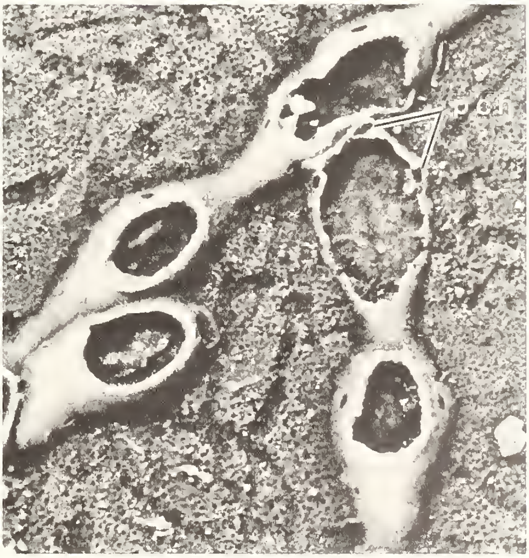

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LIDGARD, *Monoporella*, *Pyriporopsis*, *Wilbertopora* communication organs. The partitioned region is a pore chamber, and the part of the exterior body wall adjacent to it contains an uncalcified window, which forms a potential budding site (Banta 1975; Gordon and Hastings 1979).

Budding begins with the expansion by growth of the uncalcified exterior wall adjacent to the pore chamber. Expansion beyond the limits of the parental zooid transforms the pore chamber into what can then be regarded as part of the bud. The pore chamber will eventually form the proximal end of the completed zooid, confluent with its body cavity and partitioned from the parent by the pore chamber's interior proximal wall.

Unlike zooidal and multizooidal budding the growth process in intrazooidal budding is typically discontinuous. Completion of a mature zooid marks a pause in development before the expansion of a new bud. Expansion and formation of pore chambers at the distal and lateral margins of the new zooid are apparently a relatively rapid series of events. Thus complete zooids frequently appear at the colony margin; zooids at intermediate stages of development are rare.

Several previous authors have variously regarded pore chambers as heterozooids or aborted zooid buds (Silen 1944; Banta 1969; Gordon 1971*b*). In the context of the model presented here I consider pore chambers part of the parental zooid until expansion of the body wall beyond that zooid transforms them into part of a bud (see Banta 1975; Gordon and Hastings 1979). This transformation is similar in kind but reversed in polarity to that by which a multizooidal body wall becomes part of an individual zooid (Cheetham and Cook 1983). It is difficult to regard pore chambers as fully formed heterozooids (Gordon 1971*b*), since the chamber will often be confluent with the body cavity of the new zooid and body walls are continuous through the proximal part of that zooid. Silen (1944) regarded lateral pore chambers in multiserial colonies as aborted buds that were prohibited from forming zooids by the presence of adjacent lineal series. This view is not consistent with the observation that, in uniserial colonies, most lateral pore chambers never develop into zooids, yet presumably have the potential and space to do so.

Finally, pore chambers can be compared with the ascophoran hypostegal coeloms that are associated with frontal budding. Both structures are essentially coelomic chambers partitioned from the perigastric coelom by interior walls containing communication organs. Most workers have considered the hypostegal coelom to be an integral part of the zooid rather than an aborted bud, especially in species that do not form frontal buds. Even in those species that do bud frontally the space occupied by the hypostegal coelom and the calcified frontal shield are considered part of the parental zooid until the frontal wall begins to expand. After expansion begins these parts belong to the body cavity and basal wall of the frontally budded daughter zooid, a transformation equivalent to that in distal or lateral intrazooidal budding.

Uniserial colonies with intrazooidal budding often have virtually the same geometric arrangements as colonies with zooidal budding (text-fig. 8A), as can be seen by comparing *Pyriporopsis* and *Allantopora* (Pl. 28, fig. 5; text-fig. 4). Lineal series are separate and interserial communication organs rare or absent. New series are budded distally or laterally from pore chambers with intraserial communication organs.

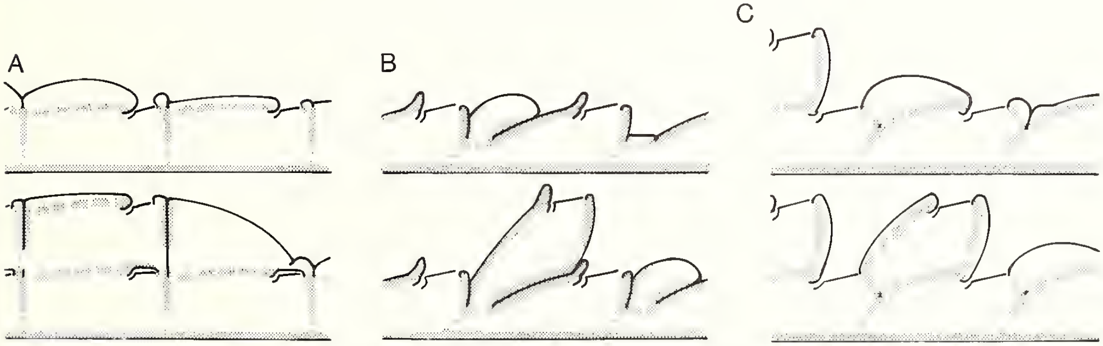
Coalescent budding is commonly present in multiserial colonies of most species with intrazooidal budding, even among the earliest species with multiserial geometries that appeared in the early Cretaceous (Pl. 28, fig. 6; text-fig. 8B). Zooids formed by intraserial budding develop directly at the growing edge of a colony in such a way that the timing of budding events in adjacent zooids rarely coincides. Gordon's (1971*a*, *b*) studies of budding in *F. malusii* (Audouin) suggest that bud fusion may occur at any time prior to calcification, forming complete zooids wherever space permits, regardless of lineal series relationships. Multiserial colonies may also exhibit discrete lineal budding; within a given colony, both geometries may be present and occur repeatedly (Pl. 28, fig. 1).

MULTILAYERED BUDDING

Geometries

Mound-like colonies in cheilostomes result from one of two kinds of growth. Most such colonies grow by multiserial frontal budding of successive layers of zooids. The underlying layers are partially or completely cut off from the environment, but physiologic connections may be maintained with the new outer layers. Many-layered colonies may also be formed without frontal budding by new encrusting layers partially or completely overgrowing pre-existing layers; the frontal surfaces of underlying zooids are completely sealed and vertical connections are absent. Self-overgrowth evidently depends on single-layered budding processes, sometimes modified in ways that I will consider in the next section.

Simple lineal geometries. Uniserial frontal budding, though possible, is apparently absent in encrusting species. However, erect uniserial groups such as the Scrupariidae may bud frontally (Harmer 1957). In colonies with *discrete multiserial* frontal budding, buds generally arise from upward growth of the frontal membranous cuticular wall that covers the hypostegal coelom (that part of the body cavity above the calcified frontal shield) (Pl. 29, figs. 1, 2; text-fig. 9A). The expanding hypostega forms the bud that is destined to become the new zooid (Banta 1972). In *S. floridana* (Osburn) the bud expands over the cuticular operculum and fuses with a distal portion of the hypostegal coelom, becoming confluent between the points of cuticle insertion on the distal, proximal, and lateral walls of the underlying zooid (Pl. 29, fig. 3). The operculum is covered by a segment of exterior wall that overlies a superopercular space. As the bud enlarges, calcified exterior walls grow upward from the lateral (exterior) and transverse (interior) walls of the parental zooid (Pl. 29, fig. 4). Interserial communication organs develop as in single-layered growth between adjacent frontally budded zooids. The upper surface of the expanding bud will eventually form the frontal wall of the new zooid. This zooid communicates with its parent through areolae that originally linked perigastric and hypostegal coeloms. These areolae (frontal pores provided with communication organs) appear to be necessary for the possession of a hypostegal coelom in ascophorans (Banta 1973). The hypostegal coelom, frontal shield, and areolae of the parental zooid are thus transformed into parts of the new zooid. Consequently, multiserial frontal budding should be regarded as an intrazooidal process.



TEXT-FIG. 9. Budding geometries in multilayered growth. A, discrete multiserial budding in *Schizoporella floridana* (Osburn); frontal buds arise from upward expansion of hypostegal coelom in simple lineal series (modified from Banta 1972). B, discrete multiserial budding in *Celleporella hyalina* (Linnaeus); frontal buds arise from upward expansion of frontally directed pore chambers, literally overgrowing the parental zooid. C, coalescent and nonlineal frontal budding. Frontal buds formed by expansion of hypostegal coeloms in adjacent parental zooids. Buds contact and fuse to form a single daughter zooid. Note remnants of original bounding cuticle dissolved in fusion process. In some species, extensive bud fusion produces a laterally confluent budding zone in which new zooids are partitioned by interior vertical walls and lineal relationships are lost. All are longitudinal sections through parental and frontally budded zooids; interior and exterior walls depicted as in text-fig. 1.

A new colony surface is produced with each generation of frontally budded zooids. With access to the environment reduced or totally lacking, covered zooids can no longer be fully functional. Feeding organs soon begin to degenerate but some tissues remain viable long after the overlying layer is complete. Zooids in successive layers are connected through communication organs that provide pathways for nutrient regression during periods of environmental stress (Cummings 1975). Successive generations form closely packed columns of zooids, each column a vertical lineal series contacting along double exterior walls. New vertical lineal series begin with the formation of an interior vertical wall bisecting a developing bud to form two smaller zooids (Pl. 29, fig. 3; Banta 1972). Each zooid will subsequently give rise to a separate vertical lineal series, budding new zooids in the normal manner. This aspect of frontal budding in *Schizoporella* is in some ways analogous to ordinary row bifurcation in single-layered multiserial growth.

Zooids in successive vertical generations frequently lose the polarity of the quincuncial arrangement in the original layer and appear to be oriented at random. However, quincuncial order may be re-established by formation of a new encrusting layer on the colony surface. Frontally budded zooids may subsequently bud 'laterally', eventually forming an encrusting layer of zooids that may cover some or all of the colony surface. The interaction of self-overgrowth and frontal budding often makes the history of a colony's development seem extremely complex.

Celleporella hyalina (Linnaeus) grows by discrete multiserial frontal budding even though lacking a hypostegal coelom. Frontal buds develop from frontally directed pore chambers located near the proximolateral margins of the zooids (Pl. 29, figs. 5–7; text-fig. 9B). The upper body wall of the pore chamber is an uncalcified membranous cuticle. As the membranous wall of the pore chamber grows upwards the bud expands distally and overgrows the calcified frontal wall of the parental zooid. A calcified skeletal layer is deposited in the exterior walls of the bud as it advances over the parent and matures to become a recumbent zooid. Interserial communication organs may develop between laterally adjacent frontally budded zooids by a process inferred to be the same as in single-layered growth. Bud fusion is not necessarily precluded, but in areas where developing zooids were clearly visible, coalescent budding was not observed.

The frontal buds in *Celleporella* are intrazooidal because they are partitioned from the parental zooid by the pre-existing interior wall that floors the pore chamber (Pl. 29, fig. 7; Gordon and Hastings 1979). The pore chambers communicate with the perigastric cavity of the parental zooid

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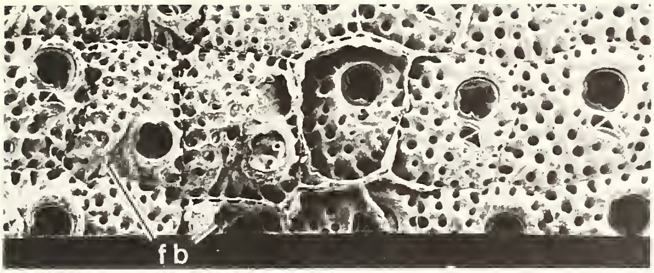
EXPLANATION OF PLATE 29

Figs. 1–4. *Schizoporella floridana*(?) (Osburn), USNM 376705, Cedar Keys, Florida, Recent. 1, frontal skeletal surface showing frontally budded zooids (fb) arising from individual parental zooids in the underlying layer of the colony, × 40. 2, side view of fig. 1, showing internal skeletal morphology and lineal relationship between zooids in successive layers (note continuity of vertical walls between layers); budding geometry is discrete multiserial; budding process is intrazooidal, × 40. 3, detail of frontal bud showing partially developed vertical walls conforming to frontal outline of parental zooid; at bottom, vertical wall (vw) of another bud bisects the frontal surface of the underlying zooid, presumably forming two daughter buds and initiating a new vertical lineal series, × 75. 4, detail of exterior vertical wall of frontally budded zooids and interior transverse wall of parental zooids (note the lack of cuticle in the lower portion followed by the inception of exterior cuticle (cut) in the upper portion); cuticle originally inserted only at the frontal wall boundary between adjacent zooids in the underlying layer, then grew upward during bud expansion, × 440.

Figs. 5–7. *Celleporella hyalina* (Linnaeus), USNM 376706, Whiting River, Maine, Recent. 5, frontal skeletal surface showing frontally budded zooids, calcified walls of frontal bud (fb) at an early stage of development, and uncalcified windows of frontally directed pore chambers (pch; chambers themselves are not visible), × 160. 6, side view of fig. 5 showing internal skeletal morphology of parental and overlying frontally budded daughter zooid and skeletal pores connecting adjacent zooids at both levels within the colony; budding geometry is discrete multiserial; budding process is intrazooidal, × 160. 7, detail of frontally directed pore chamber (pch) showing interior wall with pore plate and inception of cuticle (cut) in exterior walls of frontally budded zooid, × 375.



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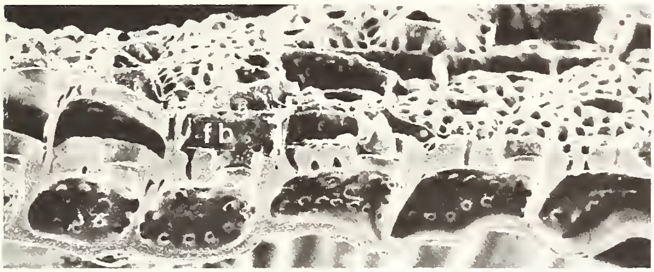

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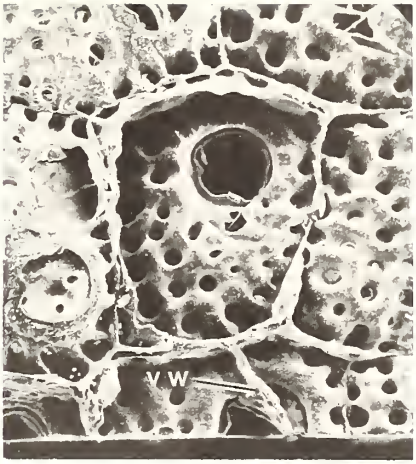

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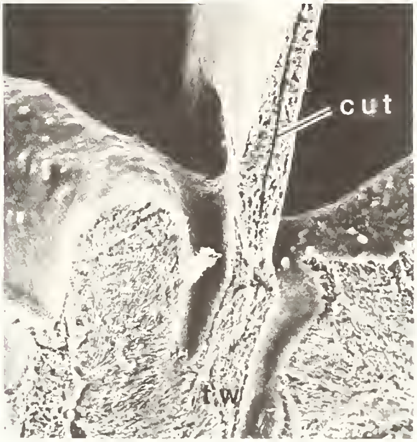

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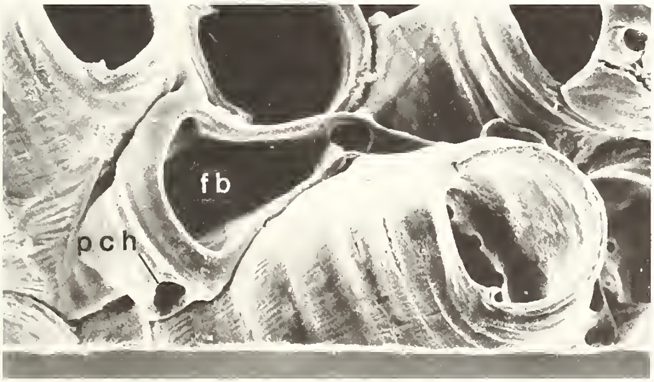

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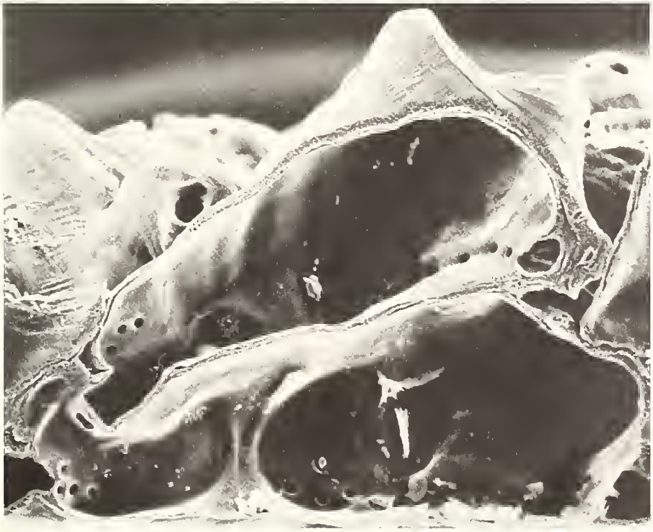

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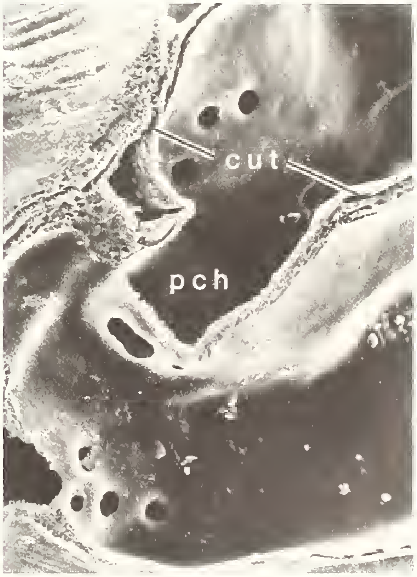

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LIDGARD, *Schizoporella*, *Celleporella* through communication organs developed in their interior walls. The sequence of wall formation can be observed directly behind the growing edge of the colony; the floor of the chamber is completed prior to the completion of the zooid.

Coalescent and nonlineal geometries. These multiserial geometries occur together in many ascophoran cheilostomes. Frontal buds in *Stylopoma spongites* (Pallas) and other similar species originate from the hypostegal coeloms of two or more adjacent parental zooids, generally at the same vertical level in the colony. The frontal walls of the parental zooids swell upward, contact one another, then fuse by dissolution of the intermediate cuticles (Pl. 30, figs. 1, 2; text-fig. 9c). The now coalesced bud continues to develop above its parents, forming vertical exterior skeletal walls as it grows. Areolae that originally connected perigastric and hypostegal coeloms now provide vertical connections to the developing zooid. As in simple lineal frontal budding the areolae, frontal shield, and hypostegal coelom become parts of the bud at the onset of body wall expansion. The transition from coalescent to nonlineal budding may occur rapidly and is often difficult to distinguish, as was found for several species of *Celleporaria* and *Stylopoma*. Bud fusion is often quite extensive, producing still larger laterally confluent budding zones that extend over the area of a number of zooids and only later become partitioned into individual zooids. New zooids formed in these zones can no longer be attributed to the coalescence of two or three lineal buds. The resulting pattern is therefore nonlineal, in which zooids are partitioned by interior vertical walls (Pl. 30, fig. 6).

Colonies that grow in this way have highly irregular frontal surfaces with functional zooids at two or more vertical levels (Pl. 30, figs. 3, 4). This irregularity is due in part to the discontinuous nature of intrazooidal frontal budding. The process of bud fusion permits new zooids to develop wherever space permits, even directly above the operculum of a zooid at some lower level (Pl. 30, fig. 7). Transitions from coalescent to nonlineal budding also confound the interpretation of vertical wall formation; cuticle insertions are visible around the margins of some zooids, whereas in others they are not (Pl. 30, figs. 4, 5). The latter are presumably formed completely by interior walls in confluent budding zones. This complex developmental pattern totally obscures vertical lineal relationships and creates the jumbled and seemingly random orientations of zooids in frontally budded layers.

Based on a preliminary survey of several hundred encrusting species, coalescent and nonlineal geometries appear to be the dominant mode of frontal budding in cheilostomes. The development of

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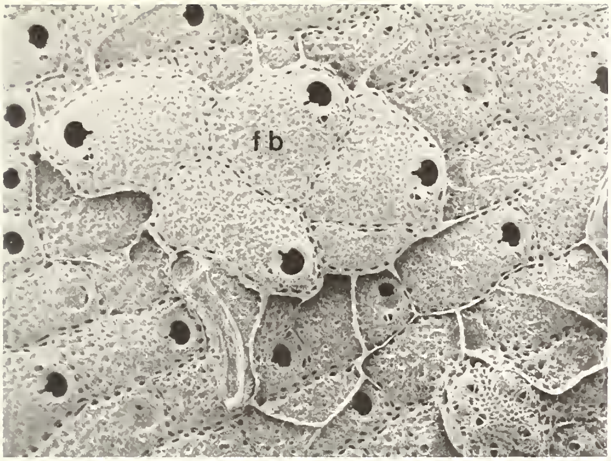
EXPLANATION OF PLATE 30

Figs. 1, 2. *Stylopoma spongites* (Pallas), USNM 376707, Rio Bueno, Jamaica, Recent. 1, frontal skeletal surface with frontally budded zooids (fb) (note lack of conformity between quincuncially arranged zooids in underlying layer and frontally budded zooids formed by bud fusion); budding geometry is coalescent multiserial; budding process is intrazooidal, ×25. 2, calcified vertical walls (vw) of partially developed frontally budded zooids frequently traverse the frontal surfaces of several underlying parental zooids; calcified basal walls partially separate the body cavities of developing frontal buds from the cavities of underlying zooids by covering frontal pores, orifices (or), and ovicells (ov), ×60.

Figs. 3–7. *Celleporaria magnifica* (Osburn), USNM 376708, North Carolina, Recent. 3, frontal skeletal surface with typically irregular arrangement of functional zooids and frontal buds at several vertical levels; frontal bud (fb) at right centre showing internal pore openings that connect both vertically and laterally to adjacent zooids; budding geometry is predominantly nonlineal; budding process is intrazooidal, ×40. 4, side view of fig. 3, showing internal skeletal morphology (note striking lack of conformity between basal (bw) and vertical (vw) body walls of frontal bud at left and frontal and vertical walls of underlying zooids), ×40. 5, detail of cuticle insertion (cut) in colony frontal surface; the transition between coalescent and nonlineal budding geometry is inferred to represent an increase in the lateral extent of fusion among frontal buds of contiguous zooids; as the zone of bud fusion extends beyond the boundaries of identifiable parental zooids, lineal relationships are no longer recognizable, ×500. 6, interior vertical wall of a bud prior to completion of pore plate (ppl), ×230. 7, portion of calcified basal wall covering the orifice (or) of an underlying zooid, ×170.



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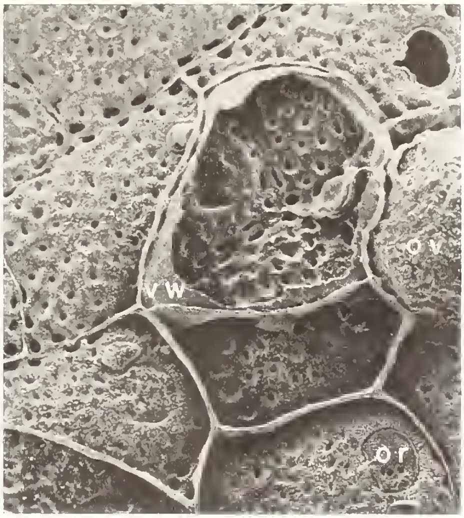

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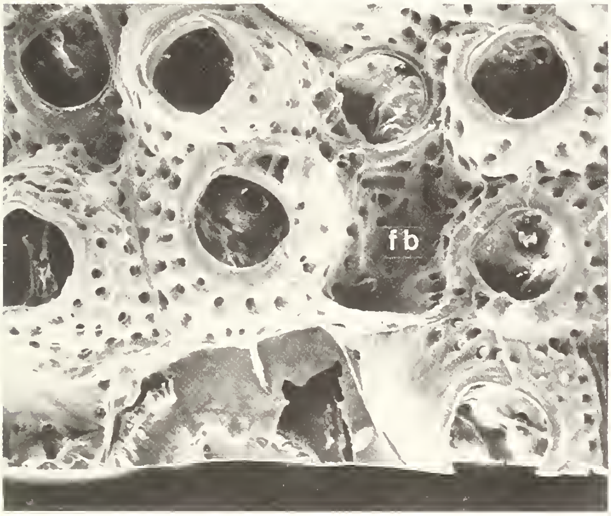

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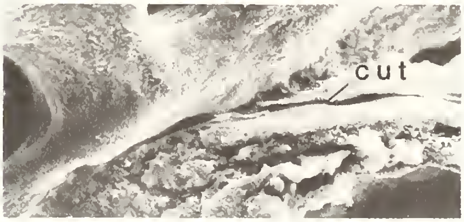

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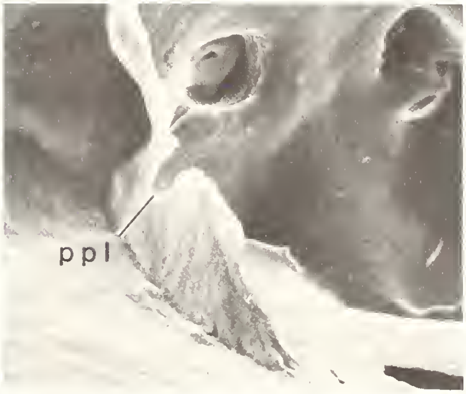

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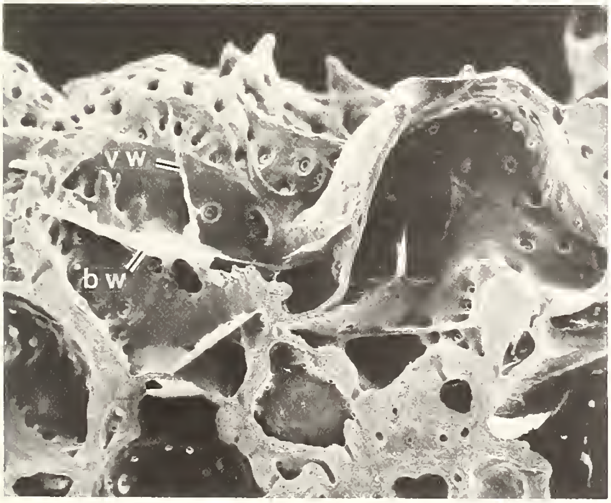

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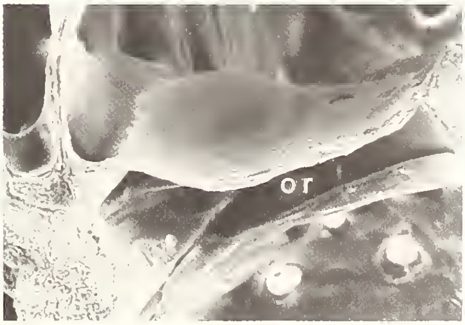

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LIDGARD, *Stylopoma*, *Celleporaria*

a confluent budding zone in species with frontal budding is analogous in many respects to the formation of extrazooidal parts in *Metrarabdotos* (Boardman and Cheetham 1973). A second analogy may be drawn with nonlineal single-layered growth in the Cupuladriidae (Hakansson 1973) and Euthyrisellidae (Cook and Chimonides 1981*a*). Some species with nonlineal frontal budding show little or no evidence of a transition from a coalescent geometry. This is particularly true for a number of conescharelliniform and orbituliporiform species that develop rootlets and never grow beyond a few zooids in size (Cook and Chimonides 1981*a*, *b*). In species such as *Sphaeropora fossa* (Haswell), zooids formed by frontal budding beyond the ancestrular stage are partitioned almost entirely by interior walls.

Processes

It was shown above that the frontal budding process in encrusting cheilostomes is intrazooidal (text-fig. 1B). Frontal budding by zooidal or multizooidal processes may not be viable. Should the entire frontal surface be expanding in a manner analogous to that in single-layered growth, new zooids would be partitioned 'proximally' to the expanding frontal surface and would therefore be completely separated from the external environment prior to their completion. This apparent prohibition of zooidal and multizooidal frontal budding should, however, be treated with caution until complex architectures of frontal budding in erect groups such as scrupariids have been more fully investigated.

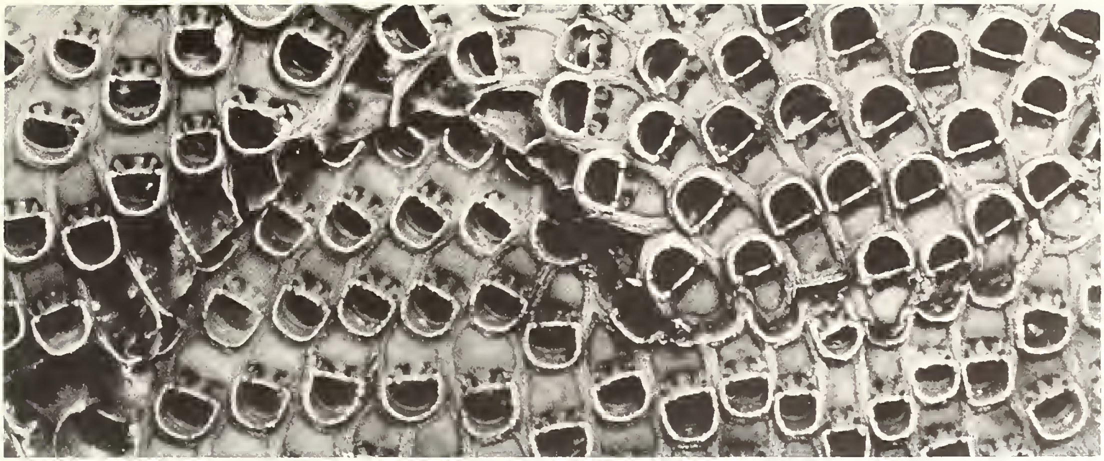
The capacity for frontal budding has been considered previously to depend on the presence of areolae and a hypostegal coelom covering the frontal shield (Banta 1973). While this is generally the case, frontal buds can also develop from structures not associated with the hypostegal coelom, as in *Celleporella hyalina* (Linnaeus) which lacks both areolae and hypostega. The ability to bud frontally from frontally directed lateral pore chambers is apparently an independent evolutionary accomplishment. An indication that comparable structures have evolved in other groups is found in the Catenicellidae (Banta and Wass 1979). While they do not bud frontally, some species in this group develop an extrazooidal skeleton from laterally situated coelomic chambers provided with communication organs. In any event, frontal budding does appear to be restricted to ascophorans with partitioned coeloms connected through intrazooidal communication organs. In the great majority of cases, frontal buds arise from a hypostega separated from the main body cavity by a calcified frontal shield.

Hypostegal coeloms in anascans are not fully partitioned in that they lack communication organs and are confluent with the perigastric cavity through opesia or opesiules. The lack of hypostegal coeloms with communication organs appears to represent a constraint to the development of frontal buds. Anascans have, however, circumvented frontal budding to produce multiple layered colonies. Different groups have evolved modifications of single-layered budding processes and geometries that enable colonies to overgrow their own frontal surfaces.

EXPLANATION OF PLATE 31

Fig. 1. *Steginoporella* sp. nov. Jackson, 1979*a*, USNM 376709, Rio Bueno, Jamaica, Recent; zooids regenerated from injured region on right grow above the level of injured zooecia, subsequently re-establish discrete multiserial geometry, and encrust the original colony surface; light photograph of stained specimen coated with ammonium chloride, × 12.

Figs. 2–5. *Antropora tincta* (Hastings), USNM 376710, Hancock Sta. 396–t114, Western Pacific, Recent. 2, frontal skeletal surface of colony, × 60. 3, side view of fig. 2 showing internal skeletal morphology; zooid on right with pores connecting to two daughter zooids (centre) at different levels in the colony, × 60. 4, detail of interior transverse wall without cuticle (note pores (p) connecting parental zooid with under- and overlying daughter zooids), × 140. 5, upper skeletal surface of colony showing early development of a self-encrusting layer of zooids, × 28.



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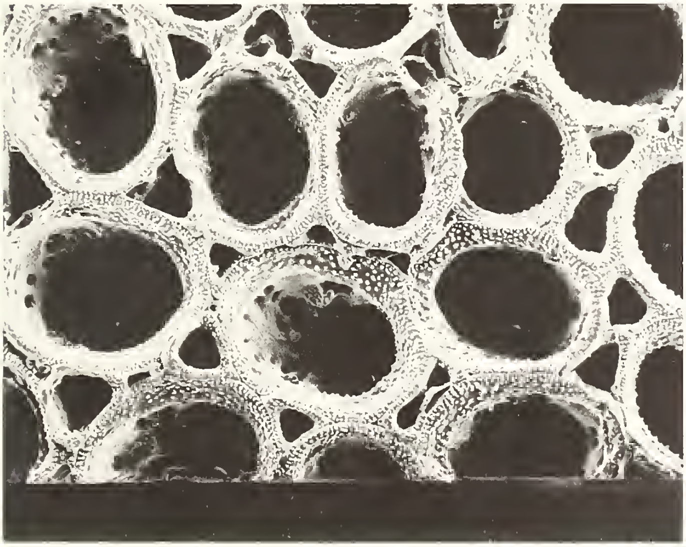

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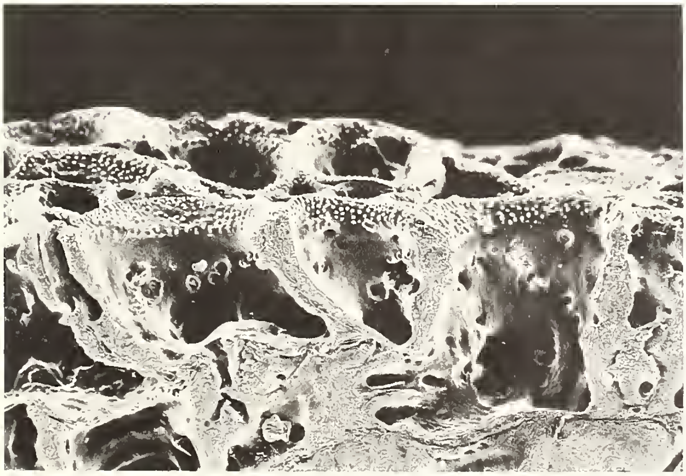

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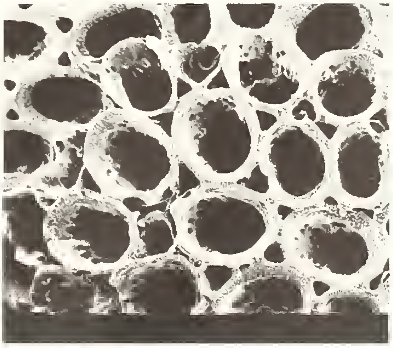

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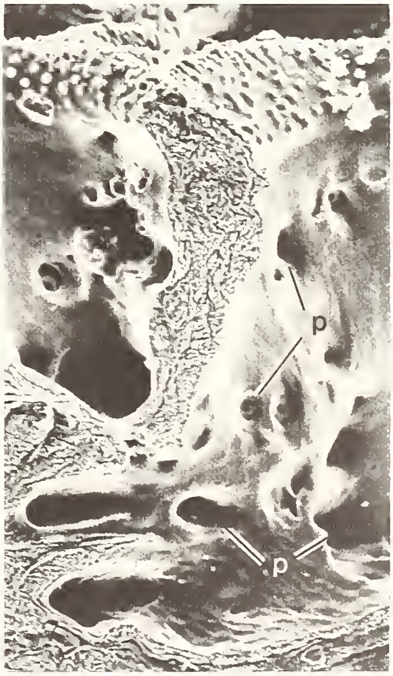


4

LIDGARD, *Steginoporella*, *Antropora*

Self-encrusting growth. New encrusting layers in ascophoran cheilostomes may develop from frontally budded zooids or, in many anascans, from an original encrusting layer in which two regions of the growing edge have become juxtaposed, enabling one to overgrow another. Reparative budding introduces another variation to self-overgrowth, occurring frequently in species such as *Membranipora arborescens* (Canu and Bassler). Budding is initiated from the communication organs of zooids surrounding an empty zooecium (in some cases the result of injury or predation). If more than one bud develops, fusion will occur to produce a single confluent bud. The bud's exterior walls lie against the inner surfaces of the zooecium and will eventually be extended above the zooecium (Pl. 31, fig. 1). A new encrusting layer develops by subsequent single-layered growth, generally re-establishing a quincuncial pattern. This process differs significantly from polypide regeneration because it involves development of new exterior walls. Separate zooid margins (sometimes including gymnocyst or cryptocyst) of the original and resurrected zooids can be easily distinguished. In some cases, zooid regeneration occurs over broad areas, and re-growth produces a subsequent overgrowing layer. Self-overgrowth by reparative budding frequently occurs among anascans that lack hypostegal coeloms connected to the perigastric cavity by areolae. Although intrazooidally budding species also undergo reparative budding, I have found no evidence of self-overgrowth by this process.

Antropora tincta (Hastings) initiates new encrusting layers in a very different way. Two daughter zooids, one atop another, are budded from the same parent but at apparently different times (Pl. 31, figs. 2, 3). The developmental sequence can be inferred from the positions and lineal relationships of parent and daughter zooids. *Antropora* produces successive generations of distal zooids by multiserial zooidal budding. During or after this process some zooids continue to grow vertically, extending their vertical walls above the frontal surfaces of distally adjacent zooids (Cook, in press). This subsequent expansion is possible without budding because of the simple membranous frontal wall of the completed zooid. Expansion of a second distal bud begins, growing over the frontal surface of the first daughter zooid (Pl. 31, fig. 4). This upper zooid also apparently develops by zooidal budding. It will eventually cover the underlying zooid with an exterior basal wall and may potentially give rise to a new encrusting layer.

The temporal sequence of these events can only be inferred indirectly. Small patches of self-encrusting zooids are widely distributed over the colony surface, often at some distance from the distal growing edge of the underlying layer (Pl. 31, fig. 5). These patches may begin to develop at the growing edge, then cease to grow as the edge advances. Alternatively, the new encrusting layers may develop from parental zooids that resume their vertical growth some time after the growing edge has moved on. The second scenario appears more likely, given that the size of the encrusting patches varies greatly, even when at similar distances from the growing edge. Local variability in zooid height (sometimes as great as three-fold within a colony) is also consistent with this hypothesis, since zooids at the growing edge are uniformly short. The potential for extensive (and possibly delayed) vertical growth gives *Antropora* an unusual flexibility in the formation of new encrusting layers. As demonstrated by Buss (1981), this flexibility can provide an important advantage in overgrowth abilities relative to competition for space. While the pattern of self-overgrowth in *Antropora* differs from that in other species, the budding processes involved are inferred to be virtually the same. Extensive vertical growth of an individual zooid does not represent a budding event; it is merely a continuation of that zooid's ontogeny.

EVOLUTIONARY TRENDS IN ZOOID AND COLONY GROWTH

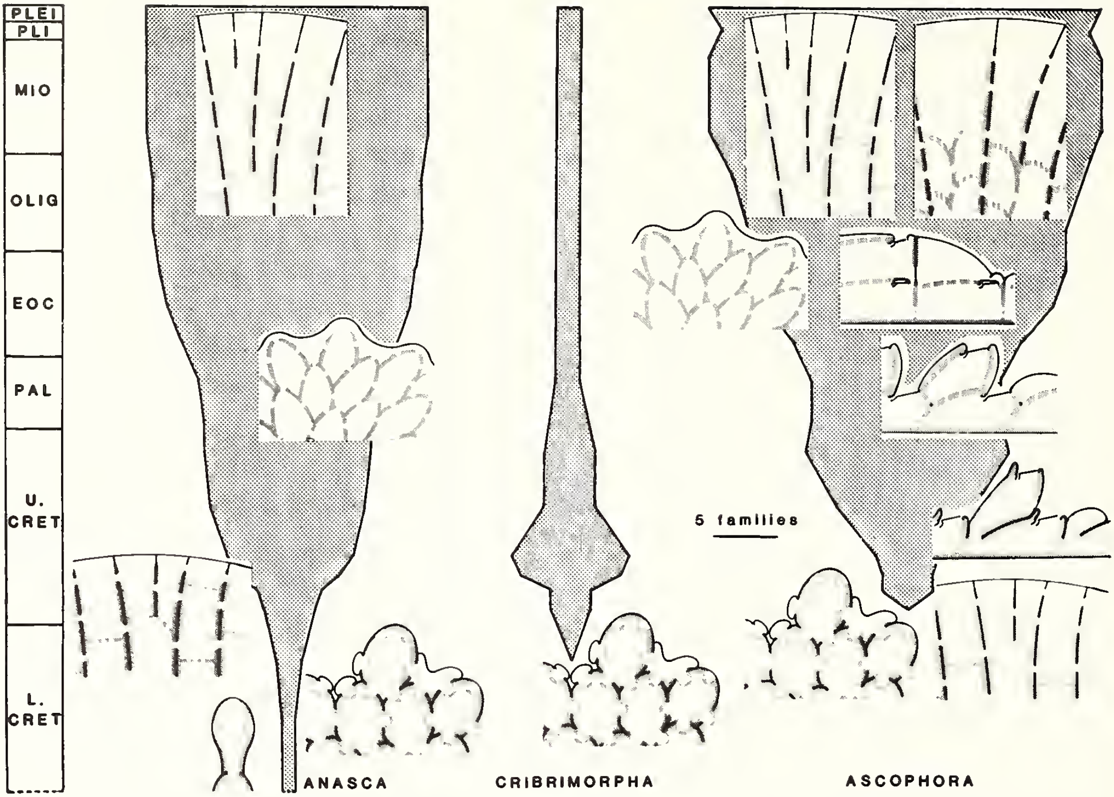
The degree to which the morphology and functions of zooids differ from that of solitary animals because of their membership in a colony expresses the degree of control that the colony has over member zooids. In cheilostome bryozoans, which as a group are exclusively colonial, these differences in colony integration represent the degree to which zooid structure and function are subordinated to colony structure and function (Boardman and Cheetham 1973; Cheetham and Cook 1983). At lower levels of integration, zooids and zooid buds retain a high degree of autonomy. At higher levels, zooid autonomy decreases and budding is influenced by more than one zooid, sometimes incorporating large sections of the colony. Thus the extensive development of interzooidal communication organs, coextensive budding zones, and partitioning interior walls indicate higher levels, while more restricted communication systems and widely developed exterior bounding walls indicate lower levels (Cook and Chimonides 1981*a*). In defining categories of budding process and geometry, I have provided a set of morphological standards for constructing a series of different levels of integration based on how colonies grow. This series is eventually testable against the occurrence of different developmental sequences in colonies preserved in the fossil record. If zooid autonomy was higher in primitive cheilostomes than in more advanced ones, as the fossil record strongly suggests, more integrated budding patterns should represent more derived rather than primitive morphological conditions.

The level of integration in individual lineages of cheilostomes, however, often seems not to have evolved in a simple stepwise progression to more highly integrated types (Boardman and Cheetham 1973). Several factors relate to this. There appears to be a broad range of integration within each major group of cheilostomes. Budding process and geometry may vary within species and even within a single colony; for example, in *Membranipora* budding is at first zooidal and later multizooidal when colonies have attained sufficient size. These mutual occurrences clearly establish that some types of budding can be transitional to others. Equally significant is the fact that a number of potential combinations of budding processes and geometries predicted by the model are not transitional. These combinations have not been found in nature. They are either undiscovered, have not yet evolved, or are in some way constrained from doing so. Geometric and developmental constraints can often be made conspicuous by determining boundary conditions of morphologies related to growth from existing colony structure. Certain other morphologies may be further restricted by conflicting functional requirements of parent and daughter zooids. Relationships between the presence or absence of certain morphological features and the ability to grow in a particular way can be established empirically by comparative study. More rigorous testing of these relationships may, however, depend on biomechanical or detailed phylogenetic analyses, often within more limited taxonomic groups (Cheetham and Thomsen 1981; Lauder 1981; Cheetham and Hayek 1983).

Perhaps most importantly the same budding processes and geometries have arisen independently many times in taxonomically distinct groups and often in different temporal sequences (text-fig. 10). These appearances strongly suggest parallel or convergent trends combined with an overall mosaic pattern of evolution in the several major stocks within the order. Until more fossil evidence is available the inferred evolutionary progression from less integrated to more integrated modes of growth can only be interpreted as a broad evolutionary pattern that cuts across phylogenetic boundaries. The most striking result is that this pattern is remarkably consistent with progressive evolutionary trends in zooid structure from simple anascan to complex anascan and cribrimorph to ascophoran (Harmer 1902); in the successive appearance of increasingly more integrated and morphologically complex structural types in the genera of the early–late Cretaceous; and in the marked diversification of taxa and of colony morphologies during the two major radiations of cheilostomes during the late Cretaceous and the Eocene (Cheetham 1971; Boardman and Cheetham 1973; Cheetham and Cook 1983, and references therein).

In this section I focus on three major evolutionary trends in encrusting growth that appear to have greatly altered the diversity of cheilostome taxa and colony forms through time: from intrazooidal to zooidal and multizooidal budding; from uniserial to multiserial budding; and from single- to multilayered growth by frontal budding. This pattern of increasing colony integration, particularly in the ways colonies grow, appears to be a dominant theme in cheilostome evolution, and indeed in the evolution of many other colonial animals (Coates and Jackson, in press). It is important to note, however, that less integrated morphologies have persisted throughout the history of the group, though they now constitute a much smaller proportion of overall cheilostome diversity.

Intrazooidal, zooidal, and multizooidal budding. The intrazooidal budding process in single-layered colonies typically corresponds to a relatively low level of colony integration, all zooids being formed principally by exterior body walls. Each zooid has morphogenetic control over certain structures



TEXT-FIG. 10. Diversity of families within the three suborders of cheilostomes from the early Cretaceous to the Recent. Similar budding processes and geometries have evolved repeatedly, even in distantly related taxa and in different temporal sequences. In many cases, initial diversification of groups with new modes of growth (shown as in text-fig. 1) correspond with periods of major increases in familial diversity, as in the late Cretaceous and Eocene. Note especially transitions from uniserial to multiserial budding in early Cretaceous anascans, appearance of zooidal budding in anascans and ascophorans in the late Cretaceous, and diversification of frontal budding in ascophorans in the Palaeocene and Eocene. Diversity data modified from Cheetham (1971) and Hakansson and Thomsen (1979), with timescale adjusted according to Berggren (1972) and Obradowich and Cobban (1975).

(i.e. pore chambers) even though those structures can eventually become part of another zooid. Intrazooidal budding presumably represents the most primitive cheilostome budding pattern, appearing in the first known Jurassic cheilostome (Pohowsky 1973) and in similar uniserial species that continued to be abundant through the early Cretaceous.

Zooidal budding evolved in late Cretaceous multiserial genera after the initial appearance of multiserial geometries in genera with intrazooidal budding (text-fig. 10). Zooidal budding radiated rapidly through anascan and ascophoran suborders; its recurrent evolution in large numbers of taxa with disparate zooid morphologies strongly suggests widespread parallelism and convergence. Taxa with zooidal budding continued to diversify throughout the Tertiary, producing a sustained, directional evolutionary trend leading to the eventual dominance of zooidal budding in both encrusting and erect cheilostomes. A lack of fossil evidence precludes all but the most general inferences of phylogenetic relationships between intrazooidal and zooidal budding. That intrazooidal budding arose and diversified in Cretaceous species long before the appearance of species with zooidal budding has been clearly established (Larwood *et al.* 1967; Banta 1975; Cheetham 1975). What remains uncertain is which of several morphogenetic transitions (i.e. intrazooidal multiserial to zooidal multiserial) occurred and whether this transition took place in simple sequence or may have happened repeatedly. One indication of repeated occurrences is present in Recent species of *Electra* where distal budding is zooidal and lateral budding intrazooidal (Silen 1944). Neither is it clear whether such transitions are reversible, as may have been the case if *Fenestrulina* (with intrazooidal budding) descended from the Microporellidae and Schizoporellidae (the latter with zooidal budding). While some degree of morphogenetic polarity is implied by increasing levels of colony integration, it may not be absolute.

Direct evidence of multizooidal budding is present in colonies of *Parasmittina* from the Pliocene of the Atlantic Coastal Plain (Lidgard, unpubl.). However, an earlier origin is likely based on the occurrence of similar skeletal morphologies related to budding in species extending back to the late Cretaceous. Many of these earlier forms are congeneric with later multizooidally budding species, and have comparable skeletal architectures and geometrical arrangements of zooids. The fragile nature of multizooidal growing edges, together with the emphasis of previous studies on zooid morphology which typically excluded morphology related to growth, may have prevented the recognition of multizooidal budding in geologically older faunas. Multizooidal budding has also apparently evolved independently in a number of distantly related anascan and ascophoran groups (text-fig. 10).

Zooidal and especially multizooidal budding represent important advances in integration in that they decouple colony growth from individual zooid ontogeny. In species with intrazooidal budding, colony growth is directly dependent on zooid growth. Exterior transverse walls delimit completed zooids at the colony growing edge prior to the onset of development of each successive zooid (Pl. 28, figs. 1, 2). In species with zooidal and multizooidal budding, colony and zooid growth proceed concurrently, but the size of the growing area of the colony and the rate of growth are no longer coincident with finite zooidal size and ontogenetic stage (Pl. 27, figs. 3, 4). In some species, interior transverse walls may not begin to develop until multizooidal buds have extended the colony growing edge several zooid lengths beyond the last completed zooid. The transition from sequential to concurrent development at zooid and colony levels can also be viewed as a key evolutionary advance, increasing both the potential rate of colony growth over the substrate and the morphogenetic flexibility of the growing edge (see below). Decoupling of colony and zooidal development also implies that pre-emption of space on the substrate by colony growth does not determine what size zooids developed there eventually must be. While this decoupling of developmental processes has increased in the course of evolution across many cheilostome lineages, it can never completely individuate the colony as the unit of growth. Colonies are still ultimately dependent on zooid development and the repertoire of zooid function to initiate and maintain colony growth.

Uniserial and multiserial budding. The early Cretaceous transition from vine-like uniserial to sheet-like multiserial colonies represents an increase in integration of growth regulation among adjacent lineal series (Banta 1975; Cheetham and Cook 1983). From the earliest cheilostomes in the Jurassic through much of the early Cretaceous, all known genera retained a morphologically simple anascan zooid structure and a uniserial budding geometry (Thomas and Larwood 1956, 1960; Pohowsky 1973; Cheetham 1975; Dzik 1975; Larwood 1975). Coincident with the evolution of multiserial forms, growth of adjacent lineal series within colonies became more or less coordinated and interzooidal communications developed between zooids in laterally adjacent series. The formation of matched uncalcified windows with pore plates or pore chambers must have depended on a level of coordination in the development of adjacent lineal series not present in uniserial budding (Banta 1975). When uniserially budded zooids come into contact they generally do so at an angle, rather than in parallel rows. Buds in physically separate lineal series more frequently abut mature zooids than other buds at the same stage of development. As is apparent in *Pyriporopsis* (Pl. 28, fig. 5), normal zooid development in one of the series commonly stops; interserial communications are rarely if ever developed.

Uniserial and multiserial geometries coexist in several closely related early Cretaceous species, all of which budded new zooids intrazooidally. While multiserial colonies of *Wilbertopora* are commonly arranged in discrete lineal series, zones of coalescent budding are also invariably present (Pl. 28, fig. 6). Coalescent budding presumably arose during the early Cretaceous with the regularization of the multiserial budding pattern in *Wilbertopora* or *Wilbertopora*-like species (Banta 1975). Coalescence depends on the close proximity of buds prior to calcification, an unlikely event in uniserial *Pyriporopsis*. The two forms overlap broadly in skeletal characteristics (Banta 1975; Cheetham 1975). In fact, early growth stages in some colonies of *Wilbertopora* are uniserial; these are succeeded by generations of zooids arranged in more typical multiserial geometries. The morphogenetic and phylogenetic transition between uniserial and multiserial forms probably initially occurred in the early Cretaceous, between *Pyriporopsis* and a *Wilbertopora*-like descendant (Cheetham 1975; Cheetham and Cook 1983).

Although uniserial colonies persisted in cheilostomes throughout the Tertiary to the present, there is little evidence that they ever constituted a major proportion of cheilostomes following the early evolution of multiserial forms. Only a few uniserial genera are known in either the cribrimorphs or the ascophorans. Uniserial and multiserial cribrimorphs are known to coexist in the late Cretaceous (Larwood 1962), but the transition from a uniserial ancestral stock to a number of multiserial descendant groups, as apparently occurred in anascans, cannot be inferred from available fossil evidence. Among the ascophorans, uniserial budding is rare and probably secondarily derived. The earliest well-documented occurrence of uniserial geometry is in the gymnocystidean species *Hippothoa flagellum* (Manzoni) from the Miocene of Europe (Morris 1980). Uniserial budding in ascophorans with cryptocystidean or umbonuloid frontal walls is extremely rare or absent.

Taxa with multiserial zooidal budding had become well established by the end of the late Cretaceous, appearing successively through parallel or convergent evolution in many anascan and ascophoran families (text-fig. 10). Zooidally budding species with coalescent and compound lineal geometries did not appear until the middle Eocene and lower Pliocene, respectively (Canu and Bassler 1923; Larwood *et al.* 1967; Lagaaij 1968). Coalescent lineal budding occurs rarely in a great many species but is only extensively developed in species of *Beania*, whose fossil record is sporadic, but extends back at least to the Eocene. *Beania* possesses a relatively unspecialized morphology whose relationship to other zooidally budded groups is obscure (but see Silen 1944). The remaining geometries form a morphologically related series based on increasing levels of colony integration. Uniserial forms lack the interserial communication organs that are regularly developed in multiserial genera. These forms are morphogenetically (but not necessarily phylogenetically) related to successively more integrated forms with discrete multiserial budding (as in *Membranipora*) and compound lineal budding (as in *Parasmittina*). Colony control increases in the latter groups as space is pre-empted by a major region of the colony rather than zooid by zooid, and is then transformed into several zooids. Interior walls similarly play a greater role in partitioning new zooids.

Multilayered growth. The development of frontal budding represents a third major evolutionary trend in cheilostome growth, following earlier transitions from the predominance of uniserial to multiserial geometries, and from intrazooidal to zooidal and multizooidal budding processes. As with these earlier transitions, frontal budding involves an increase in overall colony integration, here relative to single-layered modes of growth. Frontal budding involves the loss of full functional capability in underlying zooids, increasing colony dependence and lessening these zooids' autonomous function. Frontally budding colonies also develop an additional zone of astogenetic change, formed subsequently to the initial zone of change surrounding the first zooid (ancestrula) and extending to the following zone of repetition (Boardman and Cheetham 1973). Astogeny is the sequential development of asexual generations of zooids, beginning with the ancestrula formed at larval metamorphosis.

Discrete lineal multiserial colonies apparently first occur in late Cretaceous *Celleporella* that develops frontal buds from laterally placed pore chambers (Voigt, pers. comm.). *Celleporella* probably evolved after the initial radiation of cheilostome taxa with single-layered multiserial growth. Diversification of ascophoran species with discrete lineal frontal buds developed from hypostegal coeloms most probably began in Eocene species of *Schizoporella* (Canu and Bassler 1920). Both variations of this geometry are present in living ascophorans, although neither appear to be widespread taxonomically.

The first evidence of coalescent and nonlineal frontal budding in encrusting colonies probably occurs in Palaeocene species such as *Bathosella aspera* (Canu and Bassler), although available specimens do not permit certain determination. These geometries did not become widespread until the middle Eocene when they evolved convergently in several rooted, loosely attached genera such as *Batapora*, and in a number of mound-like genera such as *Celleporaria* that generally encrusted hard substrates (Canu and Bassler 1920; Cheetham 1966; Cook and Lagaaij 1976; see also Cook and Chimonides 1981*b*). Coalescent and nonlineal geometries continued to appear among different encrusting taxa throughout the later Tertiary and are most probably the dominant modes of frontal budding in cheilostomes. While the evolution of these budding geometries in encrusting taxa was apparently delayed until the Tertiary, the possibility of an earlier origin cannot be ruled out. Zooid morphology indicative of nonlineal frontal budding occurs in abundant erect species of '*Kleidionella*' and *Beisselina* from the Maastrichtian of Europe (Voigt 1959).

Nonlineal frontal budding decouples colony growth from the ontogeny of single zooids in a manner analogous to nonlineal and other geometries and budding processes in single-layered growth. Zooids are partitioned by interior walls in a confluent budding zone that often covers large areas of a colony's surface. In loosely attached rooted species such as *Sphaeropora fossa* (Haswell), nonlineal lateral and frontal budding begin with the first generation of zooids developed from the ancestrula and constitute nearly all subsequent colony growth. The development of frontal budding appears similarly fixed in many mound-like encrusting species such as *C. magnifica* (Osburn) that almost invariably develop frontal buds within the first few generations of zooids. However, in many species, for example *Schizoporella floridana* (Osburn), lineal frontal budding occurs irregularly and possibly as a response to limitation of substrate. Frontal budding of zooidal polymorphs such as avicularia may occur irregularly or in an almost invariant pattern. This range of variability in the development of frontal buds suggests an enormous flexibility in colony control of development, much of which may be responsive to environmental cues.

Finally, multiple layered colonies formed by extensive self-overgrowth have a fossil record extending back at least to the late Cretaceous in genera such as *Conopeum* (Kues 1983). While not necessarily involving frontal budding, this mode of multiple layered growth appears to have been regularly developed by many different groups throughout the Tertiary. As stated above, self-overgrowth depends primarily on single-layered budding processes and geometries.

DISCUSSION

Ecological consequences of encrusting growth patterns. To the extent that different budding processes and geometries do not simply express inherent developmental or structural constraints or random variation, they must reflect pressures imposed by the environment. Growth patterns which evolved convergently in lineages with phylogenetically independent sets of constraints should be especially closely linked to similar ecological traits (Jackson 1979*a*). This appears to be the case in a great many fossil and Recent encrusting species. Different combinations of budding process and geometry (text-fig. 1) correlate strongly with ecological success in different habitats, regardless of the taxonomic affinities of the species involved.

A general correlation between ecological variables and colony form has been demonstrated repeatedly (Stach 1936; Cheetham 1963, 1971; Lagaaij and Gautier 1965; Schopf 1969; Rider and Cowen 1977; and others). This relationship becomes even more striking when different modes of zooid and colony development are compared to ecological parameters, such as the stability and longevity of different substrates. For example, the majority of species with single-layered nonlineal budding geometries (some also exhibit nonlineal frontal budding) live on sand or mud bottoms rather than on hard substrates (cf. Lagaaij 1963; Cook and Lagaaij 1976; Cook 1981; Cook and Chimonides

1981*a*, *b*, 1983; Cheetham and Cook 1983; and others). Although the functional reasons are not understood, this empirical correlation suggests that nonlineal budding may not be so much the result of shared phyletic origins as the convergent development of beneficial ways of growing in similar habitats. Nonlineal geometries have evolved repeatedly in morphologically distinctive anascan and ascophoran groups with a wide range of zooidal structural complexity, apparently first occurring in the free-living Palaeocene Cupuladriidae (Gorodiski and Balavoine 1961; Cook and Chimonides 1983), and later in the free-living Eocene lunulitid *Trochopora* (Hakansson, pers. comm.). A number of conescharelliniform and orbituliporiform genera, all with nonlineal budding, also appeared in the Eocene (Cheetham 1966; Cook and Lagaaij 1976; Cook and Chimonides 1981*b*). Their small colonies develop cuticular rootlets from uncalcified regions of the body wall; the rootlets presumably anchor colonies to sand grains in the absence of hard substrates. Whereas *Cupuladria* and *Trochopora* are anascans, these rooted genera are all ascophorans. Nonlineal budding occurs again in loosely encrusting sheet-like and erect branching Euthyrisellidae, which lack a fossil record (Cook and Chimonides 1981*a*). The complex zooidal structure of this group clearly differentiates it from other ascophoran taxa with nonlineal geometries.

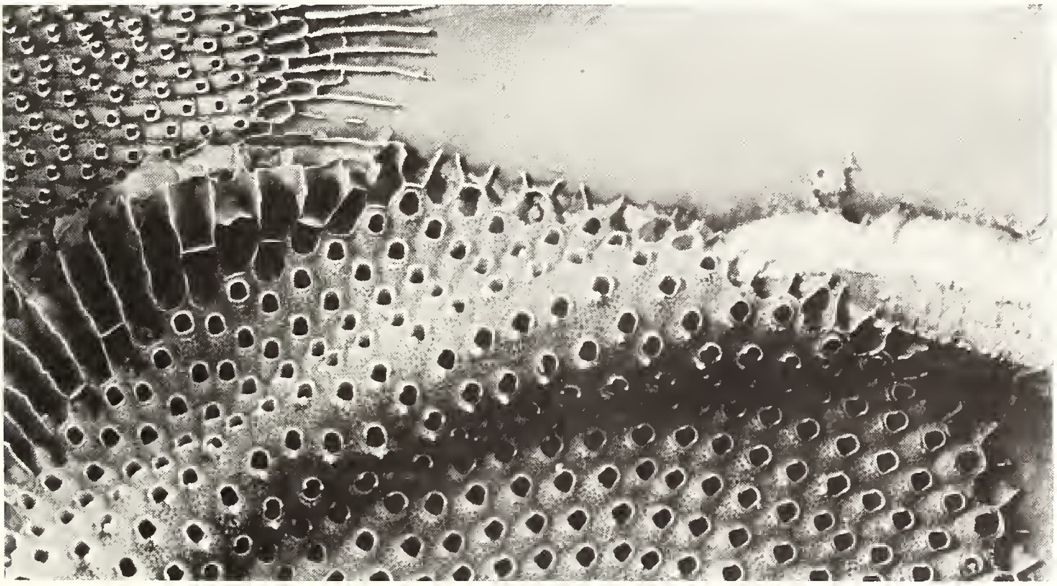
Single-layered sheet-like colonies with zooidal and commonly multizooidal budding similarly dominate cheilostome faunas on macroalgal substrates in temperate and many tropical environments (Mawatari 1975; Bernstein and Jung 1979; Jackson 1981; and others). Bryozoans often encrust all available surfaces on these ephemeral substrates; competition for space may be intense. The rapid rate of growth afforded by multizooidal budding may reflect part of a life history suited to the predictable disappearance of the substrate (Seed and O'Connor 1981; Yoshioka 1982).

Moreover, the dominant encrusting species on more stable and long-lasting substrates such as temperate-zone pilings and panels, temperate-zone cobbles and boulders, and the undersurfaces of foliaceous reef corals are frequently those with multizooidal budding, frontal budding, or both (Osman 1977; Sutherland and Karlson 1977; Sutherland 1978; Jackson 1979*b*, 1981, 1984; Kay and Keough 1981; Jackson and Winston 1982; and many others). The rapid growth and resulting increased colony size afforded by multizooidal budding have been shown to significantly increase colony survivorship in a variety of habitats (Sutherland and Karlson 1977; Sutherland 1978; Jackson 1981, 1984; Jackson and Winston 1981; and others), and also to increase long-term fecundity in many species (Hayward 1973; Hayward and Ryland 1975; Yoshioka 1982; Jackson and Wertheimer, in press; Winston and Jackson, 1984). In addition, colonies with zooidal and multizooidal budding are frequently capable of growing upward away from the substrate, overtopping a competitor and quickly overgrowing it (text-fig. 11; Jackson 1979*a*; Lidgard and Jackson 1982). Species with intrazooidal budding typically lack these overgrowth capabilities.

Frontal budding better enables a colony to overgrow potentially detrimental organisms settled on the colony surface. Vertical sections through frontally budded colonies commonly reveal secondarily encrusting organisms such as barnacles and serpulids embedded in the skeletal matrix, evidence that settlement on the colony surface is a common phenomenon. Similarly, outer layers of zooids killed by severe environmental fluctuations or predation can be regenerated from protected underlying zooids in a manner not possible in colonies that grow only as single-layered forms (Cummings 1975). Frontal budding also increases the vertical stature of the colony, better enabling it to withstand the advances of competitors and providing a vertical platform from which to overgrow their frontal surfaces (Jackson and Buss 1975; Buss 1981). Based on these observations, colonies with multizooidal and frontal budding can be expected to be relatively larger and more abundant than those with other modes of encrusting growth where competition is frequent and in stable environments where colony longevity may be at a premium. Again, these patterns of ecological dominance cut across phylogenetic boundaries.

It is not coincidental that these patterns are consistent with the evolutionary trend toward increased colony integration, both in the fossil record as new modes of growth evolve, and in modern faunas where many different modes of growth are present in species with a broad range of life history strategies (Jackson 1979*a*, 1981, 1984; Lidgard and Jackson 1982; Lidgard 1983; Winston and Jackson, 1984). In this sense, integration may be coupled with the role of the colony as the unit of selection in the environment (Schopf 1973). As cheilostomes evolved more diverse colony forms and more integrated modes of growth, the potential versatility of these new groups increased as well. Species with higher states of integration and more versatile modes of growth often retain the ability to revert to lower states as the situation demands. For example, species such as *Schizoporella floridana* (Osburn) that are capable of frontal budding may revert to exclusively single-layered growth, maximizing their allocation of resources to rapid growth across a substrate. Alternatively, mound-like frontally-budding colonies may subsequently develop zooids budded by a single-layered growth process in the act of overgrowing a competitor or an organism settled on the colony surface. Newly evolved growth patterns may have better enabled colonies to exploit new situations or face existing ecological problems, leading to the displacement of groups with less versatile modes of growth by others with higher potential versatility (Vermeij 1973*a*, *b*). Species with uniserial budding generally fare poorly in competitive overgrowth (Jackson 1979*a*) and decrease in relative abundance from the late Cretaceous onward. Diversification of multiserial taxa with zooidal and later multizooidal budding processes coincides with an increase in within-habitat abundance and with a high frequency of overgrowth success versus intrazooidally budding forms. A similar pattern apparently exists for groups with frontal budding. A vast amount of descriptive data from living and fossil cheilostome faunas tends to support these trends, but little of it provides rigorous quantitative evidence for relationships between colony integration, developmental patterns, and ecological patterns of distribution and abundance. These relationships are none the less apparent and their ecological and evolutionary consequences quite obviously important; they will be more fully explored elsewhere (Lidgard, in prep.; Lidgard and Jackson, in prep.).

Finally, we must recognize that morphological, ecological and evolutionary patterns in encrusting species are not wholly independent of those in erect taxa. While I have not attempted here to examine



TEXT-FIG. 11. *Cryptosula pallasiana* (Moll) overgrowing *Parasmittina nitida* (Verrill), USNM 376698, 376701, U.S. Fishing Comm. Sta. 5522, Vineyard Sound, Massachusetts, Recent. In the area of contact between the two species the normally zooidal budding process of *Cryptosula* has become multizooidal. The leading edge of the colony has grown upward away from the substrate, overtopping the competing colony. This appears to be a common occurrence in competitive overgrowth involving species capable of multizooidal budding. Light photograph of stained specimen coated with ammonium chloride, × 12.

budding patterns in erect cheilostomes, the eventual comparison of encrusting and erect modes of growth seems inevitable. A significant number of Recent cheilostome faunas are dominated by erect species (Lagaaij and Gautier 1965; Ryland 1974; Dyrynda and Ryland 1982), yet few have been examined in the same detail as have encrusting faunas (Jackson 1981). While encrusting colonies may respond to one suite of environmental factors, erect colonies may be subjected to a largely different suite. Encrusting colonies must contend with substrate-associated factors such as sedimentation, competitive overgrowth, or the development of feeding currents in a boundary layer flow (Cook 1977; Buss 1979; Jackson 1979*b*; Lidgard 1981; and others). On the other hand, most of an erect colony is removed from processes acting on or directly above the substrate. Erect colonies are affected by the need for branch spacing, by the risk of breakage in flow, and possibly by differential predation by fish and invertebrates (Jackson 1979*a*, 1981, 1984; Vance 1979; Bernstein and Jung 1979; Russ 1980; Cheetham and Thomsen 1981; Cheetham and Hayek 1983). Whether these implied ecological differences are reflected in differences in budding processes and geometries should provide an interesting measure of the range of variability in growth patterns that may have evolved in different selective regimes.

Some phylogenetic considerations. Bryozoans demonstrate such an enormous degree of developmental flexibility that interpreting the origins of variable developmental patterns in different taxonomic groups poses something of a dilemma. Attempts to generalize about modes of growth and to base classifications on limited suites of characters have produced a history of instability in cheilostome taxonomy (Cheetham and Cook 1983). Perceived phylogenetic relationships, especially those thought to exist among higher taxa, have been altered repeatedly to conform to the prevailing taxonomy (and preferred taxonomic characters) of the times. By giving greater weight to certain characters in a taxonomic hierarchy we may inadvertently produce apparent changes in other characters that we regard as convergent rather than non-convergent. Some of the recurrent appearances of the same budding processes and geometries in combination with different states of other characters could, in fact, reflect a natural phyletic progression rather than a complex mosaic evolution or convergence from different phyletic origins.

How then should we interpret evolutionary trends in different characters, especially those related to growth? At one level this may mean deciding which potential taxonomic characters are more variable within and between species and how much of this variability is genetically controlled. Certainly we can reasonably infer that budding processes and geometries are to some degree under genetic control. Yet species-specific characters can be tightly controlled genetically, be almost invariable intraspecifically, and yet still form a convergent or mosaic evolutionary pattern at generic and higher levels. To the extent that convergent or mosaic evolution has occurred, and I believe this has often been the case, a polythetic approach to phylogenetic relationships is likely to be most fruitful (Cheetham and Cook 1983).

At least some combinations of budding process and geometry are undoubtedly polyphyletic (text-fig. 10). It is almost inconceivable, for example, that uniserial ascophorans descended directly from uniserial anascans or cribrimorphs. Substantial differences in the overall morphology and in the respective fossil records of these groups indicate independent evolutionary origins. However, it is often unclear how much different modes of growth are constrained by phylogeny or, conversely, what constraints growth patterns place on other morphological characters. If growth patterns and other morphological characters were perfectly correlated, this would presumably reflect a hierarchical series of constraints on morphology and permit phylogenetic reconstructions based on growth patterns alone. This is decidedly not the case for the majority of cheilostome species. Individual species often possess innate flexibility in their developmental systems, so much so that the morphogenetic potential for different ways of growing is retained but rarely if ever expressed. The potential for single-layered coalescent budding, for example, is frequently present in zooidally budding multiserial colonies, but is only rarely developed, as when lineal series are constricted by an obstacle on the substrate. In some species, different budding geometries can be evoked simply by altering food sources, temperature, or water currents (Marcus 1926; Menon 1972; Winston 1976).

Differences also exist among species in the details of development and structure of homologous body walls. When different combinations of budding process and geometry occur together in a single colony, this occurrence cannot of itself demonstrate a phylogenetic pathway leading from one to another. Except in cases where there is clear historical evidence (e.g. in the *Pyriporopsis–Wilbertopora* sequence in the mid-Mesozoic), only comparative studies enable us to reasonably infer which pattern is the primitive and which the derived.

The model presented here provides a framework for comparison that should alleviate many of these difficulties. It may be that more derived modes of zooid and colony growth represent higher levels in a progressive series of states of integration in which the potential for development of some or all less integrated modes of growth is retained (e.g. coalescence in many multiserial groups). Regardless of whether these states are truly atavistic, the phylogeny of budding patterns must be interpreted with care and with these different expressions of colony integration firmly in mind.

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THE PANDERICHTHYID FISH *ELPISTOSTEGE*: A CLOSE RELATIVE OF TETRAPODS?

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ABSTRACT. The anterior skull roof and a possible postcranial skeleton of *Elpistostege watsoni* Westoll 1938 are described from the Escuminac Formation, upper Devonian, of Miguasha, Quebec, Canada. In agreement with Worobjewa (1973), *Elpistostege* is placed within the osteolepiform family Panderichthyidae. Within the osteolepiforms, the Panderichthyidae are the group closest to early tetrapods. Their skull roof pattern readily permits the transfer of tetrapod terminology to the skull roof of other osteolepiforms (contrary to Borgen 1983).

DURING the summer of 1937, T. S. Westoll acquired a skull roof from a local collector, supposedly Mr. E. Plourde of Miguasha, Province of Quebec. The incomplete dermal skull roof was published one year later without diagnosis as a 'stegocephalian' amphibian (Westoll 1938). No additional specimens were discovered over the next thirty years.

With the establishment of the Musée d'Histoire Naturelle de Miguasha in 1978, a new period of collecting and research began at the famous upper Devonian locality of Miguasha. During inventory of the collection of the late Allan Parent of Miguasha, an interesting unprepared specimen that had been collected by Parent in 1970 was discovered. Preparation by O. Bonner, Museum of Natural History, Lawrence, Kansas, revealed a skull of amphibian appearance, but with submandibular bones and a gular plate between the lower jaws, a condition found only in fish. The specimen was acquired in 1983 by the Government of the Province of Quebec for the Musée d'Histoire Naturelle de Miguasha.

The staff of the Musée d'Histoire Naturelle de Miguasha sought to collect additional material from the horizon in which the skull was thought to have been found. Their efforts were rewarded by recovery of a partial postcranial skeleton of probable panderichthyid affinities. The horizon where this skeleton was found is 87–88 m above the basal beds of the Fleurant Formation, upper Devonian. This unit is formed by pyrite-rich grey-green shales lying one to two metres below the thick sandstone-channel complex within the Escuminac Formation (Hesse and Sawh 1982). The horizon also contains *Eusthenopteron foordi*, *Scaumenacia curta* and *Bothriolepis canadensis*. That the Parent specimen (MHNM 538) may have come from this horizon is indicated by its preservation, the surrounding shales, and the pyrite content.

Depositional environment of the Escuminac Formation is considered by most authors to be freshwater/lacustrine in origin based on its tectonic position and on its fauna (Dineley and Williams 1968; Carroll *et al.* 1972; Thomson 1980; Hesse and Sawh 1982). The sedimentological features are compared by Dineley and Williams (1968, p. 252) with those of marine upper Devonian rocks of south-central New York State. The fauna, however, could be interpreted as marine, too, because most of the fishes occurring in the Escuminac Formation are found in other Devonian localities together with marine invertebrates (see Schultze in Carroll *et al.* 1972). That is the case for forms with wide distribution in the Devonian such as *Cheirolepis* (scales in marine deposits, see e.g. Gross 1973), *Eusthenopteron* (in the Baltic and Russia, Jarvik 1937; Vorobyeva 1977), *Bothriolepis* (Young 1974, 1981), and *Plourdosteus* (Obrutschew 1933; Obrucheva 1962). We tentatively interpret the depositional environment of the Escuminac Formation as coastal marine, based on the fauna present within the formation (see Schultze in Carroll *et al.* 1972).

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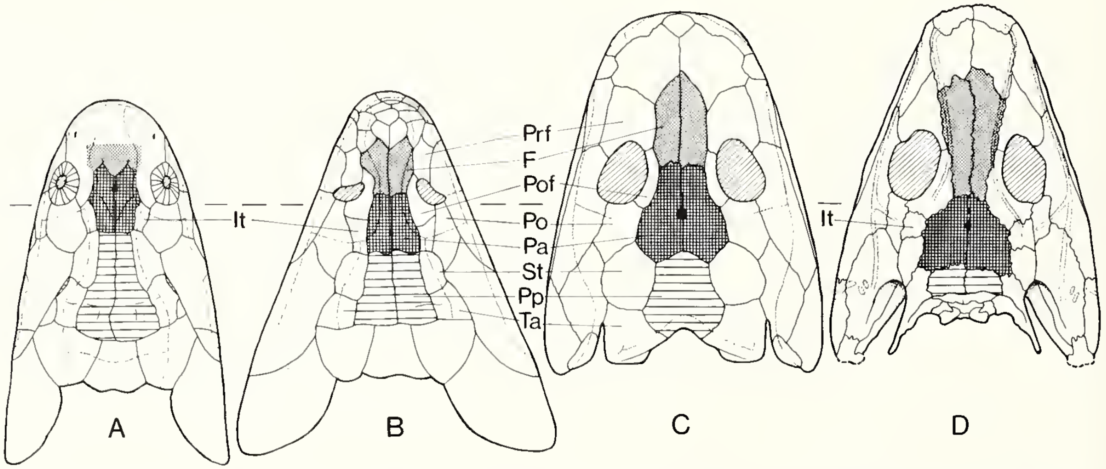
TERMINOLOGY OF SKULL ROOFING BONES

We use Westoll's (1938) terminology of skull roofing bones for osteolepiforms, contrary to the traditional terminology favoured by Jarvik (1967). Borgen (1983, Fig. 1) summarized the opposing views on the terminology of skull roofing bones. Contrary to Jarvik (1967), he accepted the traditional ('orthodox') terminology of these bones for reptilomorphs and labyrinthodonts except *Ichthyostega*. However, he followed Jarvik (1967) by insisting on the traditional terminology for these bones in *Eusthenopteron*. He could accept these contrasting traditional terminologies only:

1. by denying correlation in position between dermal bones and endocranial structures (contrary to Jarvik 1967), and between parietal foramen and parietal (as in Jarvik 1967).
2. by moving the extrascapulars of osteolepiforms onto the otico-occipital region of tetrapods. That results in a change in the correlation between frontal and parietal with underlying structures during the transition from osteolepiforms to tetrapods.

We agree with Borgen (1983, p. 744) that 'the basic criterion for homology is that of evolutionary continuity' (see similar statement in Gregory 1933, p. 92). Similarities are used to recognize homologies, and these similarities should be sought by comparison of closely related forms. Thus, by accepting a close relationship between osteolepiform rhipidistians and tetrapods (Jarvik 1967, 1972, 1980; Schultze 1970, 1977, 1981; Vorobyeva 1977*a*, 1977*b*; Borgen 1983; contrary to Rosen *et al.* 1981), we prefer to compare early tetrapods with osteolepiforms, and specifically with osteolepiforms which are probably most closely related to early tetrapods (text-fig. 1).



TEXT-FIG. 1. Terminology of skull roofing bones. Skull roof of A, *Osteolepis macrolepidotus* (after Jarvik 1972, fig. 61C), B, *Panderichthys rhombolepis* (after Vorobyeva 1977*b*, fig. 2B), C, *Ichthyostega* sp. (after Jarvik 1952, fig. 35B), and D, *Paleoherpeton decorum* (after Panchen 1970, fig. 1*a*).

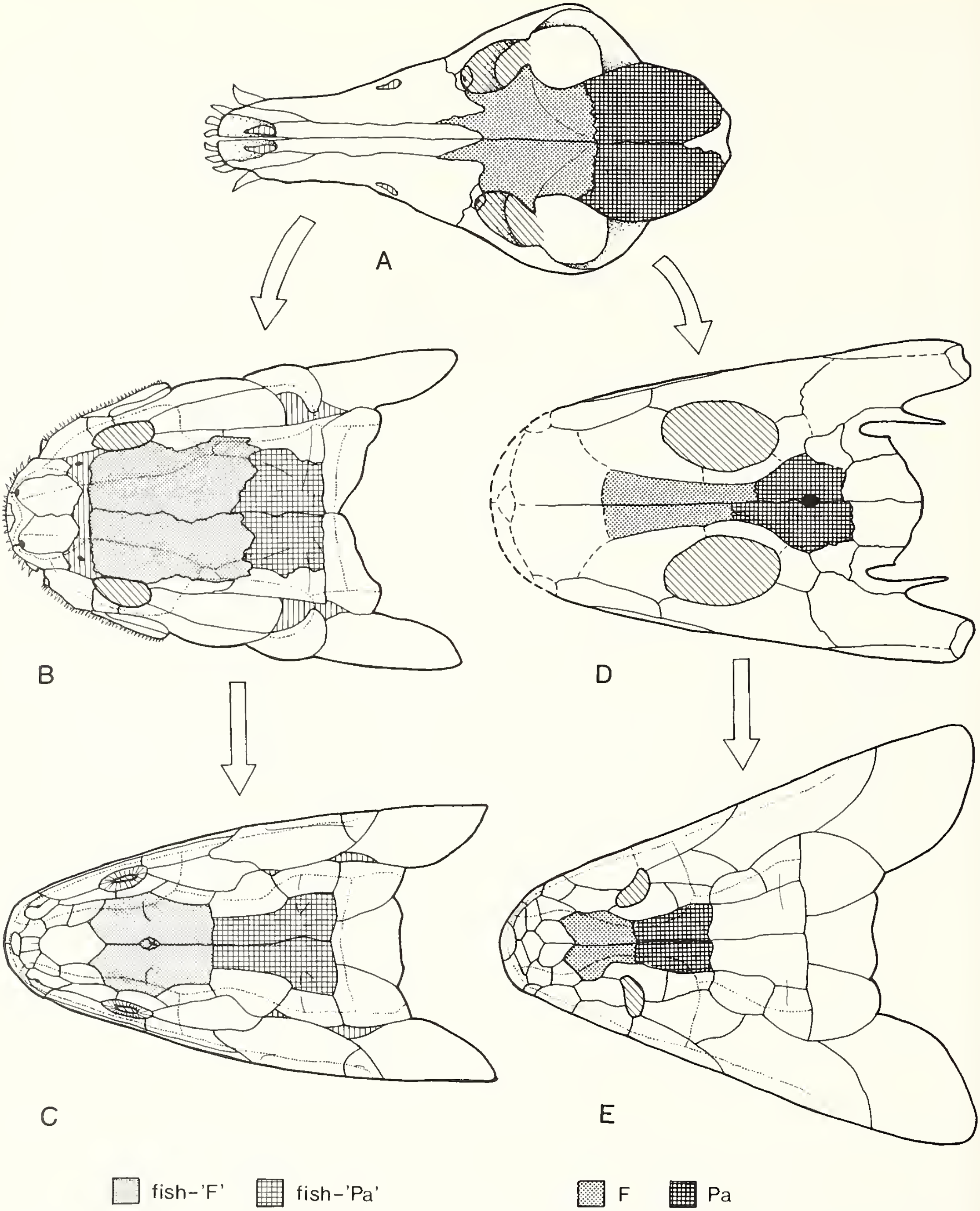
Jarvik (1967, fig. 12A, B) and Borgen (1983, figs. 2D, C, 5) showed that the same relationship exists between endocranial structures and overlying dermal bones of osteolepiforms, labyrinthodonts, and reptilomorphs. Contrary to Jarvik (1967), Borgen (1983) accepts identical terminology for skull roofing bones with the same relation to underlying endocranial structures in labyrinthodonts and reptilomorphs as does Shishkin (1973). However, Borgen did not follow Westoll (1938, 1943), Shishkin (1973) or Vorobyeva (1977*b*), all of whom applied the same terminology to skull roofing bones based on their relation to endocranial structures in osteolepiforms. Instead, Borgen made comparisons between distantly related forms (using mammals, specifically the young rabbit as did

Jarvik 1967, and *Eusthenopteron*). In mammals, despite the fact that the relationship between exocranial bones and endocranial structures varies between taxa (Parrington 1967), the exocranial bones have essentially the same relationships to endocranial structures in primitive placental mammals as in mammal-like reptiles and in early tetrapods (Parrington 1967; Borgen 1983, fig. 2A), except that the postparietals extend further anteriorly over the otic region in the earliest tetrapods. This change in position between parietal and postparietal was explained by Westoll (1943) and strongly supported by Shishkin (1973) by correlated shortening of the otico-occipital region of the endocranium and the dermal bones above it during the transition from osteolepiforms to tetrapods. A close correlation exists between endocranial structures and exocranial bones in early tetrapods and osteolepiforms. Nevertheless, Borgen (1983) refers to the bone over the otic region as the postparietal in *Paleoherpeton* and the parietal in *Eusthenopteron*, and to the bone over the exit of the optic nerve (cranial nerve II) and the basipterygoid process as the parietal in *Paleoherpeton* and the frontal in *Eusthenopteron*. The change in relationships between endocranial structures and dermal bones referred to by Borgen (1983) occurs in more advanced tetrapods; still, the relationships would hold if he had compared closely related forms.

The parietal foramen, another often disputed point in consideration of the relationship between exocranial and endocranial structures, lies between the parietals in all labyrinthodonts and reptilomorphs, independent of how far posteriorly the parietal foramen moves (Jarvik 1967, fig. 3B; Shishkin 1973, fig. 66*a–d*). In most mammals (except *Bos*, as stated by Borgen 1983, p. 742) the epiphysis (homologous to the parietal foramen) lies below the parietals. This constant relationship between parietal foramen and parietals exists throughout tetrapods. The condition in placoderms (Jarvik 1967, fig. 3A) is irrelevant. The skull roof pattern of placoderms is not comparable to that of osteichthyans and tetrapods despite Graham-Smith's (1978) attempt to construct a common ancestral pattern for placoderms and osteichthyans. We argue here for step-by-step comparison of closely related forms, but placoderms are only distantly related to osteichthyans (e.g. Denison 1978).

In early reptilomorphs and some labyrinthodonts, the postparietal lies laterally to the tabular, with the supratemporal and intertemporal lateral to the parietal; the intertemporal is lost or fused with other elements in most labyrinthodonts. The tabular and supratemporal have the same relationship to endocranial features in early tetrapods as they do in osteolepiforms (Shishkin 1973), while the extrascapulars of osteolepiforms lie behind the endocranium. Säve-Söderbergh (1932) and Borgen (1983) postulated a shift of the extrascapulars onto the skull roof in tetrapods to become the postparietals. Such a change in the position of these bones is in the opposite direction to that occurring in the phylogeny of labyrinthodonts and reptilomorphs where postparietals and tabulars moved posteriorly onto to occipital region (Panchen 1972). Borgen (1983, p. 746) gave no explanation or indication for this proposed change in relationship between dermal and endocranial structures. However, Säve-Söderbergh (1932) and Jarvik (1967) considered the position of occipital commissure to be indicative of such a transition. Changes in the position of lateral lines from one bone to another are known to have occurred in early tetrapods (e.g. Shishkin 1973) and have even been accepted by Borgen (1983, p. 750). Thus, the shift of the occipital commissure to a pair of bones anterior to the extrascapulars was possible for early tetrapods (see Graham-Smith 1978).

If we accept that homologies are best recognized in closely related forms, then Borgen's (1983) argument for the use of traditional terminology in early tetrapods and osteolepiforms can be tested by comparing forms close to the fish-tetrapod transition. These include *Ichthyostega*, *Acanthostega*, *Elpistostege*, and *Panderichthys* (text-fig. 8). Borgen (1983, p. 748/749) drew support for his use of the traditional osteolepiform terminology from the position of the 'frontals' between the orbits in mammals, reptilomorphs, and advanced batrachomorphs, i.e. the primary reason for use of the traditional terminology in fishes and osteolepiforms (text-fig. 2A, B, C). He uses contrary to his proposition to clarify what happened at this transition, a comparison between distantly related forms (i.e. position of bones in relation to the orbits in mammals and fishes). Other supporting evidence is a consequence of his acceptance of the topographic criterion for the homology of the frontal. On the other hand, the bones of *Ichthyostega* and *Acanthostega* can easily be compared with those in other



TEXT-FIG. 2. The 'traditional' way of transferring the terminology of skull roofing bones in mammals (A. *Vulpes vulpes*) to fishes (B. *Amia calva*; C. *Eusthenopteron foordi*, after Jarvik 1972, fig. 61D) and, alternatively, by comparison of forms most closely related to early amphibians (D. *Paleoherpeton decorum*, after Panchen 1970, fig. 1*a*) to panderichthyid osteolepiforms (E. *Panderichthys rhombolepis*, after Vorobyeva 1977*b*, fig. 2B).

early tetrapods (Jarvik 1952). In *Ichthyostega*, the 'parieto-extrascapular' of Jarvik (1972, 1980) and Säve-Söderbergh (1932) lies over the otico-occipital region as does the postparietal in early tetrapods and the 'parietal' of Jarvik (1972, 1980) in osteolepiforms. Borgen (1983) argues that there is no close functional or embryological correlation between skull roofing bones and endocranium. That permits the change in their position relative to each other from osteolepiforms to reptilomorphs and to mammals as postulated by Westoll (1943). Still, the constant topographic relationship between endocranial structures and related dermal roofing bones in closely related forms is a more reliable indication of bone homology than a topographic relation to the orbits alone. The 'frontals' of Jarvik (1967, 1972, 1980) surround the parietal foramen, as do the parietals in all other tetrapods.

Borgen (1983) presents a defence of two opposing terminologies, one derived from phylogenetic step-by-step comparison from mammals back to early tetrapods (text-fig. 2A, D, E). The other, he derives solely by topographic comparison between mammals and fishes (text-fig. 2A, B, C). The topographic relationships between bones and the orbits often changes during ontogeny within one species (Boy 1972, Shishkin 1973) and may also differ between members of closely related groups. For example, the rostral margin of the 'frontal' in osteolepiforms lies in front (*Eusthenopteron*, *Elpistostege*), between (*Osteolepis*, *Panderichthys*), or close to the posterior margin of the orbits (*Eusthenodon*).

In early tetrapods, the suture between frontals and parietals shifted from a position between the orbits (*Ichthyostega*, *Acanthostega*, and others) to the level of the posterior margin of the orbits (*Paleoherpeton*, *Colosteus*, *Benthosuchus*, some specimens of *Greererpeton*, and others), and finally to the most common position behind the orbits (*Greererpeton*, most labyrinthodonts and reptilomorphs). Contrary to Borgen (1983, p. 744), a posterior, not a forward movement of this suture relative to the orbits has been observed in ontogenetic series of *Branchiosaurus*, *Micromelerpeton*, *Sclerocephalus*, and *Pelosaurus* (Boy 1972, Shishkin 1973). In *Eusthenopteron* this suture (which equals the anterior margin of the 'frontals') moved anteriorly during ontogeny when compared to the orbits, while the parietal foramen migrated posteriorly (Schultze, 1984). Extreme ontogenetic lengthening of the postorbital region is a typical rhipidistian feature which is not paralleled in early tetrapods (contrary to Borgen's statement, p. 744).

We believe it is unnecessary to repeat all the reasons for applying the terminology of skull roofing bones used for early tetrapods to osteolepiforms (see Shishkin 1973). It follows from Borgen's (1983) presentation of the different views that the traditional terminology of either tetrapods (Westoll 1938, 1943) or osteolepiforms (Jarvik 1967) should be used in both closely related groups. The possibility of transferring, step-by-step, the widely used terminology applied to mammals, back to early tetrapods (as accepted by Borgen 1983), favours the use of the traditional tetrapod terminology for osteolepiforms and actinopterygians as employed by Romer (1945) and Jollie (1962). In addition, *Panderichthys* and *Elpistostege* have paired frontals in front of the parietals, thus making their skull roof pattern much more tetrapod-like than that of other osteolepiforms.

SYSTEMATIC PALAEONTOLOGY

Order OSTEOLEPIDIDA Boulenger 1901 correct.

Family PANDERICHTHYIDAE Vorobyeva 1968

Diagnosis (*emended*): Osteolepiform fishes with tetrapod-like skull roof pattern; paired frontals followed by paired parietals and paired postparietals, paralleled by elongate prefrontal (equals supraorbital 1), postfrontal (equals supraorbital 2), intertemporal, supratemporal, and tabular. Snout composed of many bones, medial rostral(s) followed by anterior, medial, and posterior postrostrals, three paired nasals, first nasal fused with premaxillary. Large postorbital can reach spiracular notch; cheek without extratemporal or postspiracular plate. Lateral rostral and anterior tectal surrounding the external nasal opening, the prefrontal does not reach the posterior margin of the external nasal opening. One large median gular between a series of broad submandibulars, followed by a pair of lateral gulars.—Nasal capsules close to the lateral wall of the posterior part of ethmoid; solum nasi and nasal walls well ossified; length of ethmoid about half ethmosphenoid length.—Vomers with posterior process in contact with each other; lateral ethmoidal contact of palatoquadrate absent, medial contact synchondrosal.—Anterior lower jaw with tusks; teeth with deep infolding at their base, internally polyplocodont.—Dermal bones and scales without cosmine. Lateral line canals in trabecular layer of bone, sensory pores sometimes joining in grooves. Rhombic scales with coarse bony ornamentation.—Scapulocoracoid connected by single contact with cleithrum.

Elpistostege Westoll 1938

Type species. Elpistostege watsoni Westoll 1938.

Diagnosis. Panderichthyid fish with elongate, broad, paired frontals meeting the parietals anterior to the orbits, parietals narrow between orbits expanding posterior to the orbits, postparietals embayed at posterior margin, frontals, parietals and postparietals very close to the same rostroposterior length. Long narrow prefrontals (equals supraorbital 1) reaching as far, or even further rostral, than the frontals. No separate intertemporal (probably included into postorbital), postorbital broad, jugal contact with ventral margin of orbit brief, or lacking. Rounded dorso-ventrally elongated orbits.

Time. Late Devonian.

Elpistostege watsoni Westoll 1938

Text-figures 3–7

Diagnosis. As for genus.

Type horizon and locality. Escuminac Formation, Frasnian, upper Devonian; shore of river Ristigouche at Miguasha, Province of Quebec, Canada.

Holotype. BMNH P60526a, b (posterior half of skull roof).

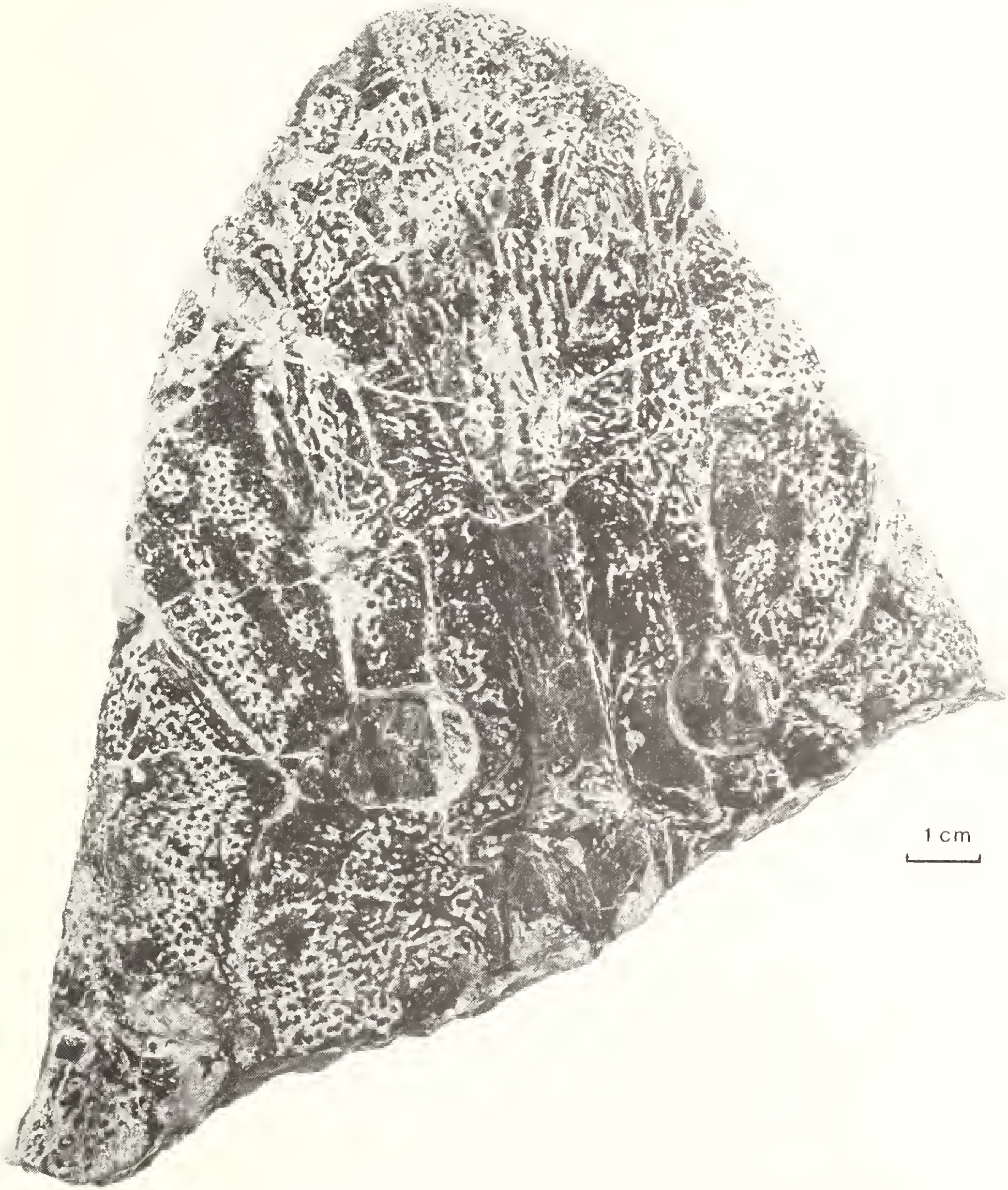
Additional material: MHNM 538 (head without posterior portion), ?MHNM 537 (postcranial skeleton without fins or head).

Description. The holotype was the only known specimen of *Elpistostege* until 1981; casts of it were used for the identification of MHNM 538. Specimen MHNM 538 will be described here before comparisons are made with the holotype.

The head of specimen MHNM 538 is flattened post-mortem so that gular plate and lower jaw are in close contact with the palate region (text-fig. 5D). The skull roof is pressed down into one plane, only the 'eye brows' are elevated above that plane. From the snout back to the posterior part of the parietals is all that is preserved of the skull. The posterior margin is broken obliquely so that the jugal is complete and the postorbital nearly so on the left side; both bones are only partially preserved on the right side. The postcranial specimen MHNM 537 is assigned to *Elpistostege* with reservation. The surface sculpture of the scales are similar to that of the skull roof of *Elpistostege*. The distance between dermal ridges on the skull roof is comparable to that of similar ridges on the anterior scales; both are 1·4–1·7 mm apart. Depth of ornament (up to 0·8 mm) is also closely comparable. Only the discovery of a complete specimen could definitely prove the association. Nevertheless, the fact that there is no other form known from the locality of Miguasha with this type of ridge and furrow dermal ornament favours our association of these two specimens.

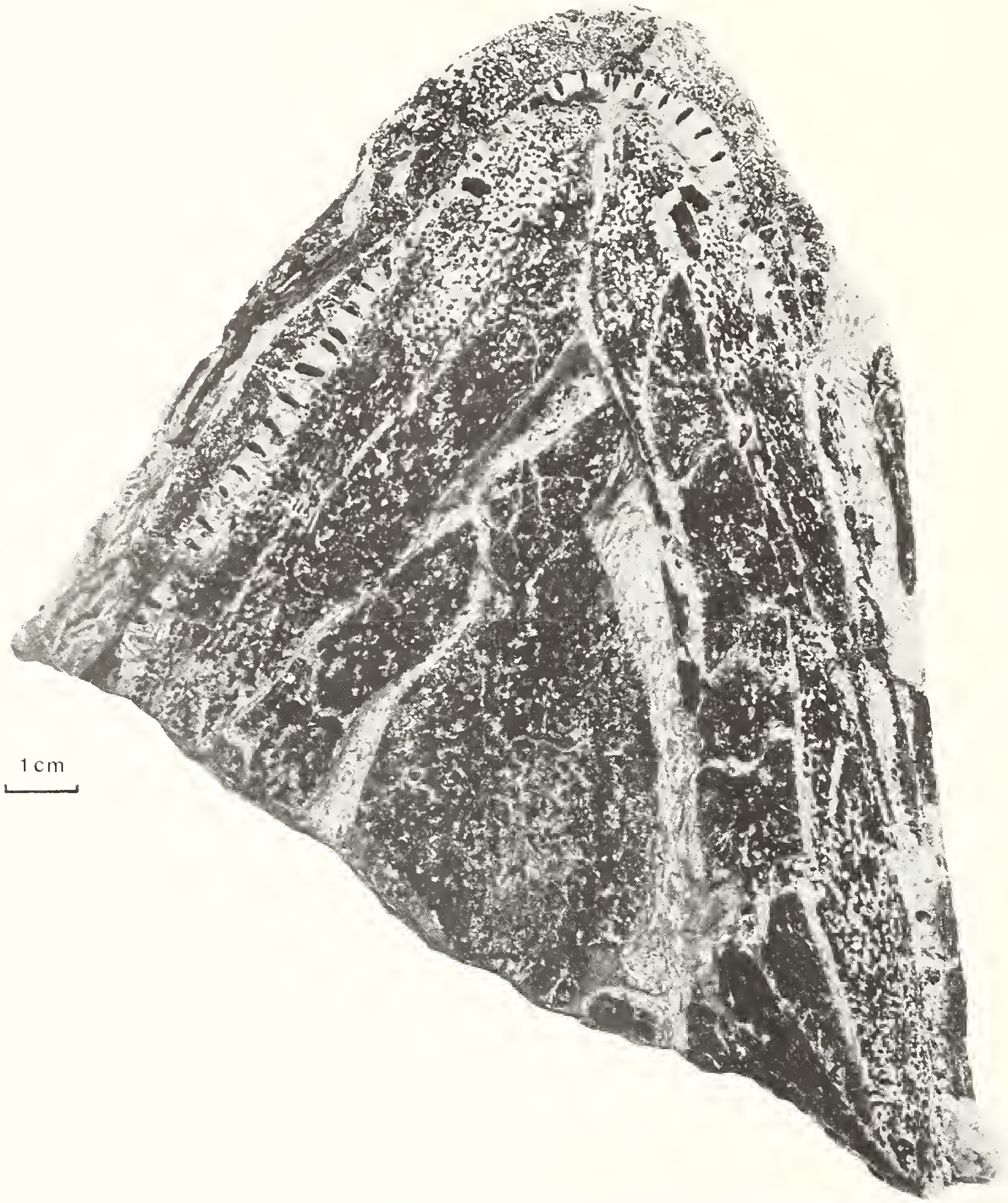
Skull roof (text-figs. 3, 5A). A tongue of the parietals extends between the elevations ('eye brows') formed by the postfrontals (equals supraorbital 2), medial to the orbits. Behind the postfrontals, the parietals extend a short lateral wing before they widen again posteriorly. The parietal foramen lies through an elevation through which the median suture between the parietals runs anteroposteriorly; lateral to it the parietals are depressed. The postfrontal forms the dorsal or medial margin of the orbit, but reaches anteriorly further than the parietal. Parietal and postfrontal border the posterior margin of the frontal. The frontal is the broadest bone of the skull roof, anteriorly widening and interdigitating with postrostral and nasal. Lateral to the frontal lies the long narrow prefrontal (equals supraorbital 1) which reaches from the anterior margin of the orbit forward to the anterior tectal, extending beyond the anterior margin of the left frontal. The snout is covered by a mosaic of bones in which all sutures are not completely distinguishable. A series of nasals, three on the left and two on the right side, surround paired posterior, medial and anterior postrostrals; together these form the roof of the snout which is elevated above surrounding elements by the tusks in the anterior lower jaw. The orbits are wider dorsolaterally than antero-posteriorly. Each orbit is situated lateral to the high ridge ('eye-brow') that runs on both sides of the parietals and frontals.

Cheek and upper jaw (text-figs. 3, 5A, C). The cheek lies in the same plane as the skull roof; it bends ventrally at the margin to the upper jaw. Most of the broad postorbital, a jugal that reaches far anteriorly, and part of the



TEXT-FIG. 3. Skull of *Elpistostege watsoni*, specimen MHNM 538; dorsal view.

squamosal are preserved on the left side, while only the anterior part of postorbital and jugal remain on the right. The postorbital widely overlaps the parietal (text-fig. 5D) which was traversed by the supraorbital sensory canal. This indicates that the parietal may incorporate the intertemporal as suggested by Borgen (1983) for *Ichthyostega*. The right jugal briefly contacts the posterolateral border of the orbit; it is separated from the left orbit by the lachrymal which borders the postorbital. The lachrymal is a large bone widening anterolaterally. At the extreme lateral border of jugal and lachrymal and near the middle of the anterior tectal, the cheek region bends sharply downwards. At this bend, the upper jaw is crushed into the ventral plane with the lower jaw.

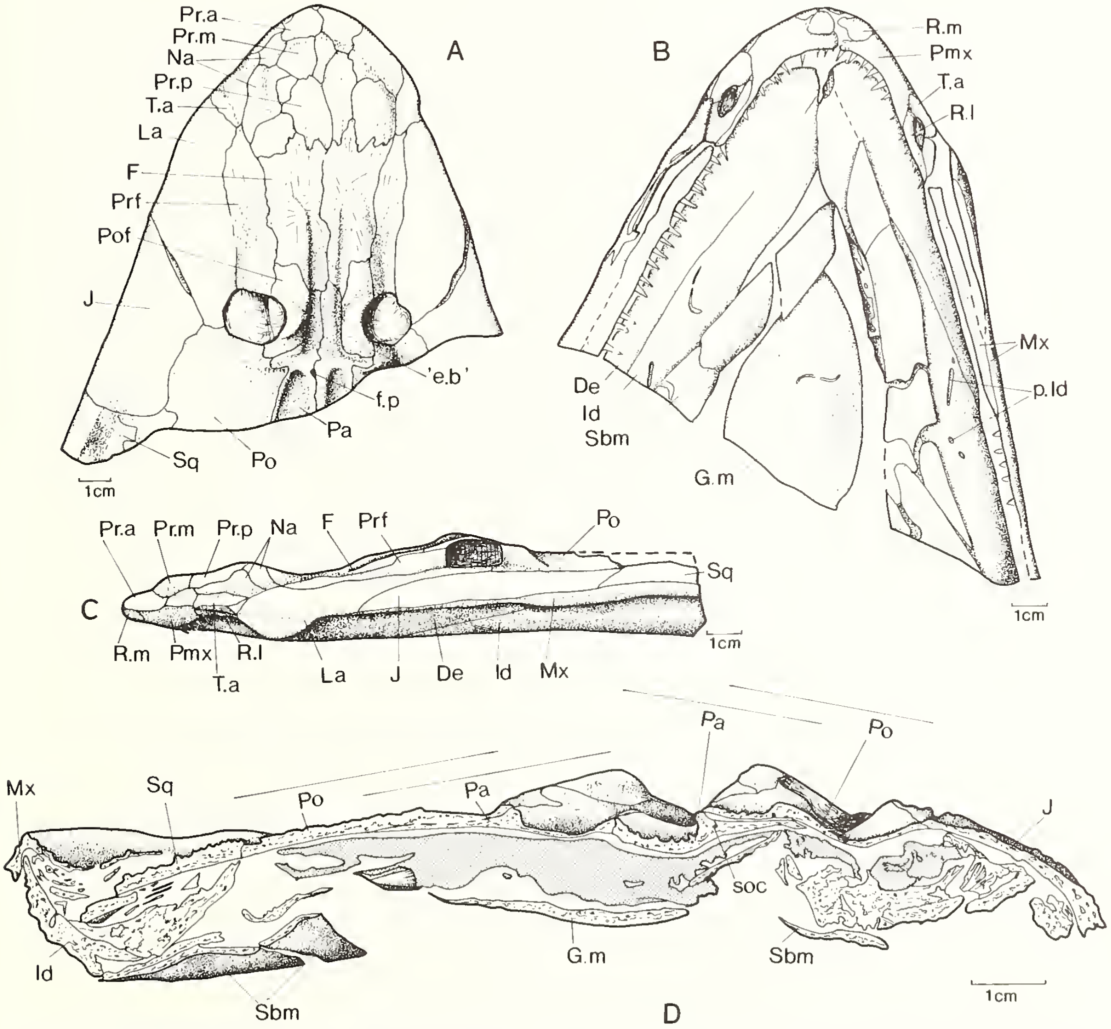


TEXT-FIG. 4. Skull of *Elpistostege watsoni*, specimen MHNM 538; ventral view.

A narrow maxilla forms the middle part of the upper jaw; it reaches to the lateral rostral which is separated from the jaw margin by a narrow posterior extension of the premaxilla. In front of the lateral rostral and anterior tectal, the premaxilla expands and then narrows again at the symphysis to accommodate a pair of median rostrals. Small, evenly spaced, pointed teeth sit on the margin of the maxilla and premaxilla.

The external nasal opening lies close to the margin of the upper jaw. It is surrounded by the lateral rostral and anterior tectal. The lateral rostral lies ventral and posterior to the nasal opening, while the anterior tectal extends from the dorsal and anterior margin of the nasal opening onto the dorsal side of the specimen, where it meets the prefrontal.

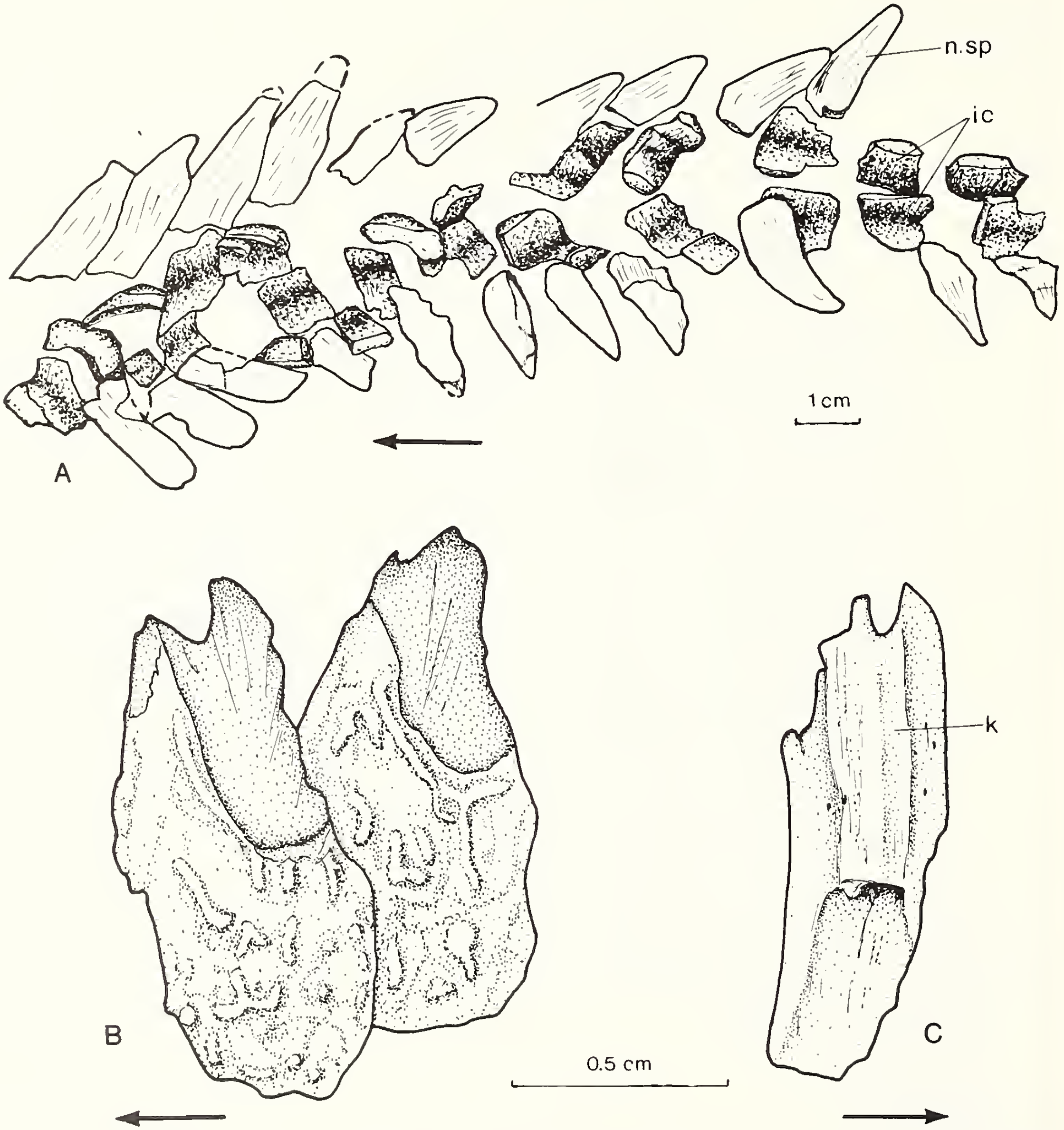
Lower jaw and gular region (text-figs. 4, 5B). The lower jaw is pressed nearly into one plane with the submandibular series and median gular plate; only the left jaw is directed upwards so that the teeth meet the teeth of the maxilla (text-fig. 5D). The boundary between dentary and infradentary series is distinguishable, but the boundaries between the infradentaries are not. Pit lines indicate that three infradentaries of the infradentary series are



TEXT-FIG. 5. Skull of *Elpistostege watsoni*, specimen MHNM 538. A, Dorsal view, B, ventral view, C, lateral view, D, posterior view (oblique cross section, on the left side further posterior than on the right; endocranial part stippled).

preserved. Three right, and four left submandibular bones lie dislocated over the lower jaw and median gular. A large median gular fills the space between the submandibular series.

Skull shape. The skull is post-mortem flattened, still it can be assumed from the cross section (text-fig. 5D) that the skull was, like that of *Panderichthys*, not greatly arched. The orbits are elevated above the skull roof with a deep depression between them. The main arching occurs close to the upper jaw; maxillae and premaxillae lie on the ventral side. The rostral part of the skull reaches far forward so that the mouth becomes subterminal. Orientation of the left lower jaw, with its oblique dorsolateral to ventromedial direction, may correspond closely to its original position. As a whole, the skull is very much like that of a labyrinthodont.

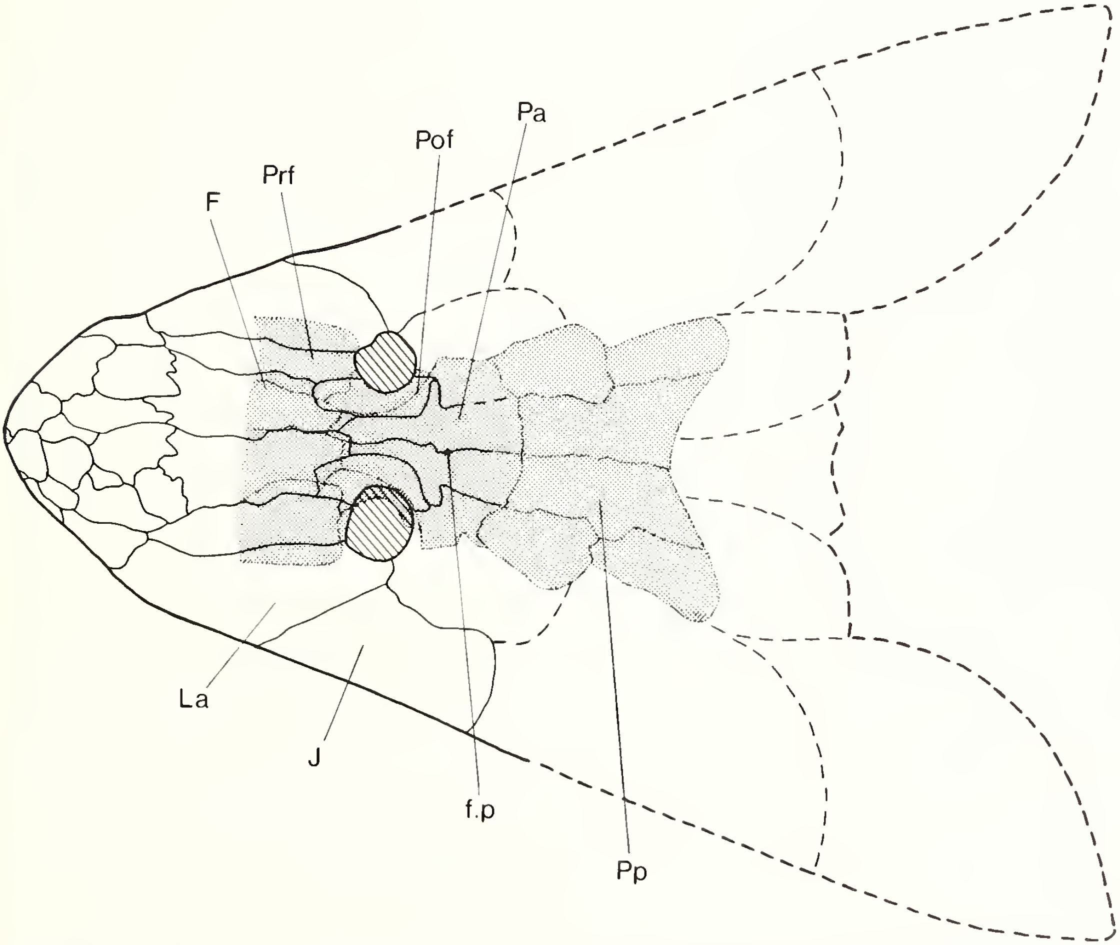


TEXT-FIG. 6. Postcranial skeleton of presumed specimen of *Elpistostege watsoni*, MHNM 537. A, Vertebrae, B, scales in external view, C, scale in internal view. Arrows point anteriorly.

Postcranial skeleton (text-fig. 6). Specimen MNHM 537 is a piece 26–27 cm long and up to 15 cm wide with scales and vertebrae. The specimen is assigned to *Elpistostege watsoni* based on the scale ornament (text-fig. 6B) which is similar to that of the skull bones (text-figs. 3, 4). Comparable rhombic scales are found on the body of complete specimens of *Panderichthys rhombolepis* (Vorobyeva 1980, fig. 1).

A string of sixteen to seventeen vertebrae runs the length of the specimen. Neural arches and intercentra (text-fig. 6A) can be identified; the neural arches, with their smooth perichondral surface, are distinct from the intercentra, which show endochondral bone tissue on the internal surface. As preserved, the vertebrae are compressed dorso-ventrally so that left and right half of the neural arches lie 'dorsal' and 'ventral' to the intercentra, which are seen from their inside or from their anterior or posterior border. The intercentra form broad half rings so that right and left intercentra together completely surround the notochord. Pleurocentra were not identified.

Portions of the scales (text-fig. 6B, C) are preserved in normal contact, and internal and external surfaces can be observed. These rhombic scales are very deep (at least twice as deep as wide). They extensively overlap each other within the dorsoventral scale rows as seen by the unsculptured part of the external side, which occupies up to half of the scale depth. The deep area, ventral to the keel on the internal surface, corresponds to the overlapped area on the external surface. Scales only narrowly overlap each other from scale row to scale row (from anterior to



TEXT-FIG. 7. Comparison of specimen MHNM 638 (solid lines) with holotype BMNH 60526 (dotted lines) of *Elpistostege watsoni*. Posterior part (broken lines) reconstructed after *Panderichthys rhombolepis* (after Vorobyeva 1977*b*, fig. 2B).

posterior). The free external scale surface is covered with irregular, strong bony ridges. On the internal surface, a distinct keel can be seen, but it does not end dorsally in a pronounced peg. The dorsal border forms a broadly based expansion ('peg') with irregular margin.

Comparison with holotype (text-fig. 7).

The holotype (BMNH P60526a, b) comprises the posterior half of the skull roof including the posterior end of the frontals and prefrontals and extending back to the posterior margin of the postparietals. The bones are seen in internal view, and were accurately figured by Westoll (1938). Specimen MHNM 538 agrees with the holotype in shape and form of the orbits, in the external ornament (preserved as an imprint in the holotype), in the position of the parietal foramen, the shape and extent of the anterior part of the parietals, and the posterior part of the frontals. These congruences and the fact that there are no other similar fish known from the Escuminac Formation at Miguasha, corroborate the assignment of the new specimen to *Elpistostege watsoni*. Differences occur in the width of the prefrontal, the postfrontal, and the posterior part of the parietal. These differences are the effect of overlap between bones because size and shape of skull roof elements varies widely between internal and external surfaces. This means that the prefrontal extensively underlies frontal and lachrymal, and that the parietal extensively underlies the postorbital (compare text-fig. 5d).

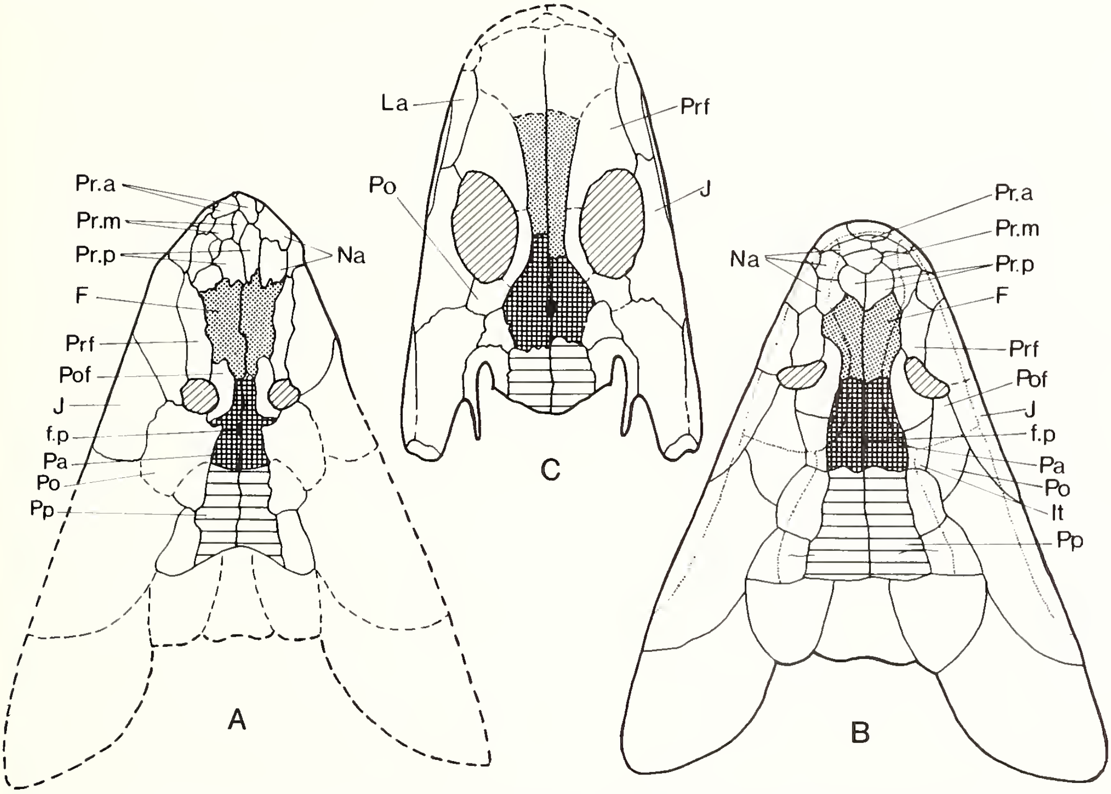
SYSTEMATIC POSITION OF *ELPISTOSTEGE*

Elpistostege was considered by Westoll (1938) as a labyrinthodont with 'a perfect transition between Crossopterygian and Ichthyostegid patterns of dermal bone'. The similarities to which Westoll (1938) referred still hold even though Vorobjewa (1973) correctly placed *Elpistostege* within the Panderichthyidae. Comparison of *Panderichthys*, *Elpistostege*, and *Ichthyostega*, with the rhipidistian, *Osteolepis*, and the labyrinthodont, *Greererpeton* (Table 1), indicates a close relationship between panderichthyids and early tetrapods, and agrees with placement of *Elpistostege* within panderichthyids (Vorobjewa 1973).

TABLE 1. Comparison of skull and cheek bones between three osteolepiforms and two labyrinthodonts

	Osteolepis	*Panderichthys*	*Elpistostege*	*Ichthyostega*	*Greererpeton*
skull roof	arched	flat	flat	flat	flat
orbits	lateral	high dorsal	high dorsal	high dorsal	high dorsal
external naris	above margin	marginal	marginal	marginal	marginal
parietal opening	between orbits	behind orbits	behind orbits	behind orbits	behind orbits
intracranial joint	external	not external	not external	not external	not external
sensory canals	in bone	in bone	in bone	in bone	in grooves
ornament	cosmine	bony ridges	bony ridges	bony ridges	bony ridges
snout shape	vertical	prominent	prominent	vertical	vertical
rostrals	?	unpaired	one pair	unpaired	none
postrostrals	?	1 pair, 2 single	3 pairs	none	none
position frontals	anterior orbits	between orbits	anterior orbits	between orbits	between orbits
frontals	?unpaired	paired, broad	paired, broad	paired, narrow	paired, long
parietals	between orbits	narrow between and wide behind orbits			behind orbits
postparietals	very long	paired, long	paired, long	unpaired, short	paired, short
anterior tectal	present	present	present	present	none
lateral rostral	present	present	present	reduced	septomaxillar
prefrontal	?	elongated	very elongated	broad	broad
postfrontal	narrow	broad posterior	narrow	narrow	broad posterior
intertemporal	present	present	missing	missing	sporadic
jugal	at orbit	at orbit	not or at orbit	wide at orbit	wide at orbit
squamosal	large	large	?large	medium	medium, long
median gular	small	large	large	none	none
submandibulars	present	present	present	none	none
operculum	present	present	present	none	none
preoperculum	present	present	present	reduced	none
extrascapularia	present	present	present	none	none

The flat skull with high dorsally situated orbits links the panderichthyids and labyrinthodonts. The external nasal opening lies very close to the margin of the upper jaw. An external intracranial joint is not developed. The parietal foramen has a position behind the orbits even though the parietals reach between the orbits as in osteolepiforms and ichthyostegids. A pair of frontals extending from between (*Acanthostega*, *Ichthyostega*, *Panderichthys*) or just in front of the orbits (*Elpistostege*) is common to all these forms (text-fig. 8).



TEXT-FIG. 8. Comparison of skull roofs of A, *Elpistostege watsoni*, B, *Panderichthys rhombolepis* (after Vorobyeva 1977*b*, fig. 2B), and C, *Acanthostega gunnari* (after Jarvik 1952, fig. 34A).

On the other hand, features such as many bones in the snout region, submandibular series, gular plates, opercular series (Vorobyeva 1977*b*), extrascapular series (Vorobyeva 1977*b*), heavy bony rhombic scales, and fins (known from *Panderichthys* only) are clearly osteolepiform piscene features of the panderichthyids. Some piscene features can still be found in ichthyostegids, such as sensory canals enclosed in bone, and an external nasal opening surrounded by the anterior tectal and lateral rostral.

The large median gular and the subterminal mouth (prominent snout) are the main features uniting *Elpistostege* with *Panderichthys*. The three pairs of nasals, anterior, medial, and posterior postrostrals, elongate prefrontals, and the elevation ('eye brows') dorsomedial to the orbits are further indication of a close relationship between these two genera. They are distinct from each other in the presence (*Panderichthys*) or lack (*Elpistostege*) of the intertemporal, the shape of parietal, prefrontal, and the postfrontal, and in the position of the suture between parietal and frontal. The jugal always reaches the orbit in *Panderichthys*, but not always in *Elpistostege*. The shape of the orbits is quite different, and the postorbital seems to be much larger in *Elpistostege*.

In conclusion, *Elpistostege* is a member of the Panderichthyidae, and the Panderichthyidae are closely related to early tetrapods. We suppose that the loss of the intertemporal occurred independently in *Elpistostege* and ichthyostegids and other labyrinthodonts many times in parallel. The single, fused postparietal is an autapomorphy of *Ichthyostega*, while paired postparietals are present in the ichthyostegid *Acanthostega*.

TABLE 2. Relation between length of frontal (fr), orbit (orb), parietal (pa), postparietal (pp), distance anterior border parietal to snout (sn), and skull roof (sk)

	sn/sk %	fr/sk %	pa/sk %	pp/sk %	orb/sk %	pp/pa %	fr/pa %
Osteolepis	32	—	23	45	18	198	—
Panderichthys	45	20	24	30	5	125	83
Elpistostege	51	29	26	22	9	84	88
Ichthyostega	50	28	26	25	19	95	108
Greererpeton	56	41	24	19	14	81	176

Relative proportions of skull bones changed at different rates in the transition from osteolepiforms to early tetrapods (Table 2). The parietal had an equal length in these forms, about one quarter of skull roof length, while the frontal enlarged gradually from panderichthyids to ichthyostegids (longer in *Acanthostega* than in *Ichthyostega*) to labyrinthodonts. The postparietal reduced its length markedly, a point especially noted by Westoll (1938, 1943). The greatest change in the relationship between length of postparietal to length of skull or parietal occurred during the transition between osteolepid and rhizodontid osteolepiforms on one hand and panderichthyid osteolepiforms and labyrinthodonts on the other. All these proportional changes reflect the change in snout proportion. The snout is longer in panderichthyids and labyrinthodonts than in other osteolepiforms. The typical ontogenetic postorbital growth in osteolepiforms is reduced in panderichthyids and labyrinthodonts. Postorbital growth in osteolepiforms is correlated with ontogenetic reduction of orbital size (Schultze 1984). *Osteolepis* (text-fig. 1A) is a small osteolepiform where the orbit size does not differ much between juvenile and adult, while it does in the large *Panderichthys* and *Elpistostege*. Ontogenetic change in the size of the orbit of *Eusthenopteron* is intermediate between *Osteolepis* and *Panderichthys—Elpistostege*. Relative size of the orbit in tetrapods is similar to that of juvenile osteolepiforms.

These gradual changes make it difficult if not impossible to identify incomplete specimens as fish or amphibian (see Jarvik's 1981 critique of Rosen *et al.* 1981). Like Westoll (1938), the authors even considered the new skull of *Elpistostege* as that of a labyrinthodont before the ventral side was prepared. *Crassigyrinus* is another incompletely known form (cheek, preorbital region, cranial roof, vertebrae) 'intermediate between . . . a typical rhipidistian . . . and the Devonian amphibian *Ichthyostega* (Panchen 1973, p. 190)'. The proportions of the skull (long postorbital region), the composition of the snout, the course of the infraorbital line, the large preopercular and squamosal are fish-like (osteolepiform features). Shape (as in *Elpistostege*) and size of orbit, narrow anterior portion of parietal (as in *Elpistostege*), posteriorly widened postfrontals (as in *Panderichthys*), size of quadratojugal, quadrate, maxilla, and premaxilla are not unquestionably tetrapod features. The prefrontal is within the size range of panderichthyids, and the ornament could not be easily distinguished from osteolepiforms devoid of cosmine. The comparably small postorbital, the long border of the jugal with the ventral margin of the orbit, the lachrymal not reaching the orbit, the external nasal opening located away from the margin of the upper jaw, and snout not prominent, excludes *Crassigyrinus* from the Panderichthyidae, but not from other osteolepiform or rhizodont rhipidistians. Postparietals and tabulars are reduced to labyrinthodont size (Panchen 1980, fig. 8).

The 'two apparently adjacent centra' (Panchen 1980, p. 340 and fig. 9a, b) of *Crassigyrinus* are very similar to those in specimen MNHM 537, tentatively assigned to *Elpistostege*.

Campbell and Bell (1977) described a 'primitive amphibian' jaw from the late Devonian of New South Wales, Australia. It is difficult but not impossible to distinguish an osteolepiform jaw from one of an early amphibian. Campbell and Bell's (1977) reasons for placing *Metaxygnathus* within the ichthyostegids were based on the following features: size of the retroarticular process, the splint-like dentary, and the elongate and anteriorly acuminate surangular. We believe these characters are insufficient evidence of tetrapod affinities. A retroarticular process is normally missing in osteolepiforms (and in many labyrinthodonts), however, Vorobyeva (1977*b*) has figured a distinct retroarticular process in the osteolepiform *Lamprotolepis*. The ornament on the jaw of *Metaxygnathus* is fine, the symphysis weak, and the prearticular extends almost to the symphysis; these features are clearly those of a fish. Other characters found only in osteolepiforms include: a mandibular canal, enclosed by bone (no sulcus!), with three pores visible in infradentary 2 (equals postsplenial) and 4 (equals surangular), and an adsymphysial tooth plate. Distinct coronoids with tusks are typical of rhipidistians, still, they occur in some labyrinthodonts. Even though the characteristics of this lower jaw are insufficient to align *Metaxygnathus* with any specific osteolepiform, it clearly belongs within that group.

Elpistostege, *Crassigyrinus*, and *Metaxygnathus* are examples of the difficulties of distinguishing osteolepiform rhipidistians and early labyrinthodonts (Jarvik 1981). These numerous similarities of structure would be surprising convergences if they do not indicate a close relationship between rhipidistians and tetrapods.

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ABBREVIATIONS

In text-figures: De, dentary; 'e.b.', 'eye-brow' (elevation medial to orbit); F, frontal; f.p, parietal foramen; G.m, median gular; Id, infradentary; It, intertemporal; i.c, intercentrum; J, jugal; k, keel; La, lacrimal; Mx, maxilla; Na, nasal; n.sp, neural spine; orb, orbit; Pa, parietal; p.ld, pit-line of infradentaries; Pmx, premaxilla; Po, postorbital; Pof, postfrontal; Pp, postparietal; Pr.a, anterior postrostral; Pr.m, median postrostral; Pr.p, posterior postrostral; Prf, prefrontal; R.l, lateral rostral; R.m, median rostral; Sbm, submandibular; soc, supraorbital canal; Sq, squamosal; St, supratemporal; T.a, anterior tectal; Ta, tabular.

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TAXONOMY AND EVOLUTION OF THE CAINOZOIC SPATANGOID ECHINOID *PROTENASTER*

by KENNETH J. MCNAMARA

ABSTRACT. The spatangoid echinoid *Protenaster* Pomel, 1883, previously known only from the living Australian species *P. australis* (Gray, 1851), is described from the Tertiary for the first time. Three fossil species are recognized from southern Australia: the late Eocene *P. preaustralis* sp. nov.; the late Oligocene *P. philipi* sp. nov.; and the early Miocene *P. antiaustralis* (Tate, 1885), which is fully described and figured for the first time. *P. australis* is redescribed and the ontogenetic development and intraspecific variation documented. *Protenaster* is shown to have been a morphologically conservative genus throughout the Tertiary. The only significant morphological evolution involved the peramorphic evolution of the phyllodal plates, which formed a peramorphocline from the Tertiary to the Recent. This peramorphocline followed an environmental gradient of coarse to fine calcarenites and reflects the adaptation of successive species to feeding on finer-grained sediments.

THE spatangoid echinoid *Protenaster* is uncommon, both as a living species and in the fossil record. Indeed, even though fossil echinoids have been described from the Tertiary rocks of southern Australia since the mid-nineteenth century, and the living species *P. australis* has been known since 1851, the existence of fossil species of this genus has hitherto not been recognized. The rarity of extinct species of *Protenaster* is illustrated by the fact that of the three species described below, two are each known from nine specimens, while the third is known from only two specimens. This latter species was originally described as *Linthia antiaustralis* by Tate (1885). In addition to describing these fossil species, the living *P. australis* is redescribed on the basis of thirty-four Recent and three fossil specimens. Intraspecific and ontogenetic changes are documented in this species for the first time.

Although the genus is shown to range from the late Eocene to Recent, all four species show a remarkable overall morphological similarity to one another. Close examination for distinguishing characters has revealed an interesting evolutionary change in the nature of the phyllodal plates. Phyllodes are broad ambulacral areas surrounding the peristome in which pores are more concentrated and, particularly in spatangoids, larger than other adoral ambulacral pores; the ambulacral plates which bear such pores are termed phyllodal plates. Ontogenetic analysis of *P. australis* has highlighted the close correspondence between both ontogenetic and phylogenetic development of the phyllodal plates; these changes are quite substantial when contrasted to the overall phylogenetic morphological changes, and are analysed here.

Little attention has been paid to the ontogenetic development of the phyllodal pores and their associated periporal areas in echinoids. The phyllodal periporal areas in *Protenaster* undergo appreciable morphological change, during both ontogeny and phylogeny. Four basic states are recognized, and a terminology to describe them is introduced:

1. *Bridged interporal partition*. In this state the interporal partition is arched over the pore, effectively creating a pair of isopores which unite immediately beneath this bridge (text-fig. 5.1).
2. *Breached interporal partition*. The condition where the interporal bridge is breached medially and a unipore thus develops (text-fig. 4.6).
3. *Reniform periporal area*. The two separated interporal segments migrate adaxially and reunite to form a swollen, reniform ridge beneath which, on the adaxial side, the unipore is located (text-fig. 4.1).

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4. *Platform periporal area.* The flat, abaxial part of the periporal area swells and forms a raised platform. This may, in the largest specimens, unite with the reniform segment to form one large platform, or more usually the two may be separated by a depression (text-fig. 1A). Occasionally, a minute opening into the test, connecting with the large unipore, may be established in this depression.

MATERIALS AND METHODS

This paper is one of a series of revisions (McNamara and Philip 1980, 1984; Kruse and Philip, in press) of the fossil spatangoid echinoids of southern Australia currently being undertaken, largely on the basis of collections made in recent years by R. J. and F. Foster. These collections, and others on which this study is based, are housed in the Tasmanian Museum (TM), Museum of Victoria (NMV), Melbourne University, Geology Department (MUGD), South Australian Museum (SAM), Western Australian Museum (WAM), University of Western Australia (UWA), and British Museum (Natural History) (BMNH).

Measurements were made with a vernier calliper to an accuracy of 0.1 mm. A number of parameters are expressed as percentages of maximum test length (%TL). Where the terms 'adaxial' and 'abaxial' are used, they refer to the axis of the test.

SYSTEMATIC PALAEONTOLOGY

Order SPATANGOIDA Claus, 1876
Family SCHIZASTERIDAE Lambert, 1905
Genus PROTENASTER Pomel, 1883

Type species. Desoria australis Gray, 1851, pp. 132–133; by original designation.

Emended diagnosis. Apical system ethmolytic, with four genital pores; positioned well anterior of centre. Petals sunken; anterior pair transverse, or nearly so. Ambulacrum III sunken, bearing closely spaced pore pairs with prominent interporal partition. Peripetalous fasciole runs close to ambitus anteriorly and is indented between paired petals. Lateroanal fasciole present. Peristome sunken. Pores in phyllode isopores or unipores; periporal area raised. Second plate of interambulacrum 1 generally abutting both ambulacra I and II adorally.

Assigned species. P. australis (Gray, 1851), *P. antiaustralis* (Tate, 1885), *P. synapticus* (Henderson, 1975), *P. preaustralis* sp. nov., and *P. philipi* sp. nov.

Remarks. Mortensen (1951, p. 224) recognized the similarity of *Protenaster* to *Prenaster* but considered the two taxa to be generically distinct, primarily on account of the course of the peripetalous fasciole. This extends below the ambitus close to the peristome in *Prenaster*, whereas in *Protenaster* it runs close to the ambitus across ambulacrum III. Fischer (1966) preferred to regard *Protenaster* as a subgenus of *Prenaster*. More recently, Henderson (1975, p. 19) placed *Protenaster* in synonymy with *Prenaster*. Henderson's course of action was based in part on his belief that *Protenaster* is only known from a living species, whereas *Prenaster* is restricted to Eocene to Miocene strata; the two taxa, therefore, lying at either end of a morphological-time continuum. However, three fossil species which compare closely with the living species of *Protenaster* are known from the Eocene–Miocene of southern Australia. Furthermore, one of these species (from the late Eocene Tortachilla Limestone) coexists with a species of *Prenaster*. Henderson further considered that a species which he described as *Prenaster synapticus* (from the Eocene of New Zealand) was morphologically intermediate between *Protenaster* and *Prenaster* because it lacked an anterior notch, an attribute of *Protenaster* but not of *Prenaster*. It must be pointed out, however, that the specimens described by Henderson (1975, p. 20) are small, being less than 20 mm test length. Specimens of comparable size of Australian Eocene and Recent species similarly lack an anterior notch or, if present, it is only very weakly developed. During growth, however, the notch deepens to varying degees in different species as ambulacrum III and the petals deepen (see below). Henderson has observed that *P. synapticus* compares with *Protenaster australis* in the anterior course of the peripetalous fasciole. Consequently, I can see no justification for placing *Protenaster* in synonymy with *Prenaster*.

The two genera were contemporaneous during part of the Tertiary and followed quite separate phylogenetic pathways. *Protenaster* can be distinguished from *Prenaster* by its possession of deeper petals; a deeper ambulacrum III, in which well-developed pore pairs occur; an anterior notch; and a peripetalous fasciole which is indented between the anterior and posterior petals, and which does not extend below the ambitus anteriorly.

In addition to including *Prenaster synapticus* in *Protenaster*, *Linthia antiaustralis* Tate, 1885 is also included. This species is morphologically very similar to the living species *P. australis*. Certainly *Protenaster* is similar to *Linthia* and is likely to have evolved from it in the early Tertiary; indeed, *P. australis* was placed in *Linthia* by Agassiz (1872–1874), Tenison Woods (1878), and Hall (1904). However, *Protenaster* can be distinguished from *Linthia* by its more anteriorly positioned apical system, its broader plastron, and the bisection of the first two plates in interambulacrum 1a by the second plate of interambulacrum 1b adorally.

Protenaster australis (Gray, 1851)

Plate 32; Plate 33, figs. 3, 4; text-figs. 1, 2

1851 *Desoria australis* Gray, p. 133.
1855 *Desoria australis* Gray; Gray, p. 58, pl. 6, fig. 2.
1872 *Linthia australis* (Gray); Agassiz, p. 138, pl. 19, figs. 7–9; pl. 21, figs. 5–7.
1874 *Desoria australis* Gray; Lovén, pp. 16, 54, 57, 63, pl. 28.
1883 *Protenaster australis* (Gray); Pomel, p. 36.
1891 *Linthia australis* (Gray); Ramsay, pp. 43, 56.
1904 *Linthia australis* (Gray); Hall, p. 73.
1914 *Linthia australis* (Gray); Alexander, p. 112.
1914 *Linthia australis* (Gray); Clark, p. 169.
1917 *Protenaster australis* (Gray); Clark, p. 169.
1925 *Protenaster australis* (Gray); Clark, p. 201.
1925 *Protenaster australis* (Gray); Lambert and Thiéry, p. 520.
1928 *Protenaster australis* (Gray); Clark, p. 479.
1938 *Protenaster australis* (Gray); Clark, p. 429.
1942 *Protenaster australis* (Gray); Cotton and Godfrey, p. 226.
1946 *Protenaster australis* (Gray); Clark, p. 364.
1951 *Protenaster australis* (Gray); Mortensen, pp. 208, 224–226.
1975 *Protenaster australis* (Gray); Henderson, pp. 19–21.
1983 *Protenaster australis* (Gray); McNamara and Bryce, pp. 73–74.

Diagnosis. Phyllodal pores unipores; breached periporal area in juvenile; reniform to platform in adults.

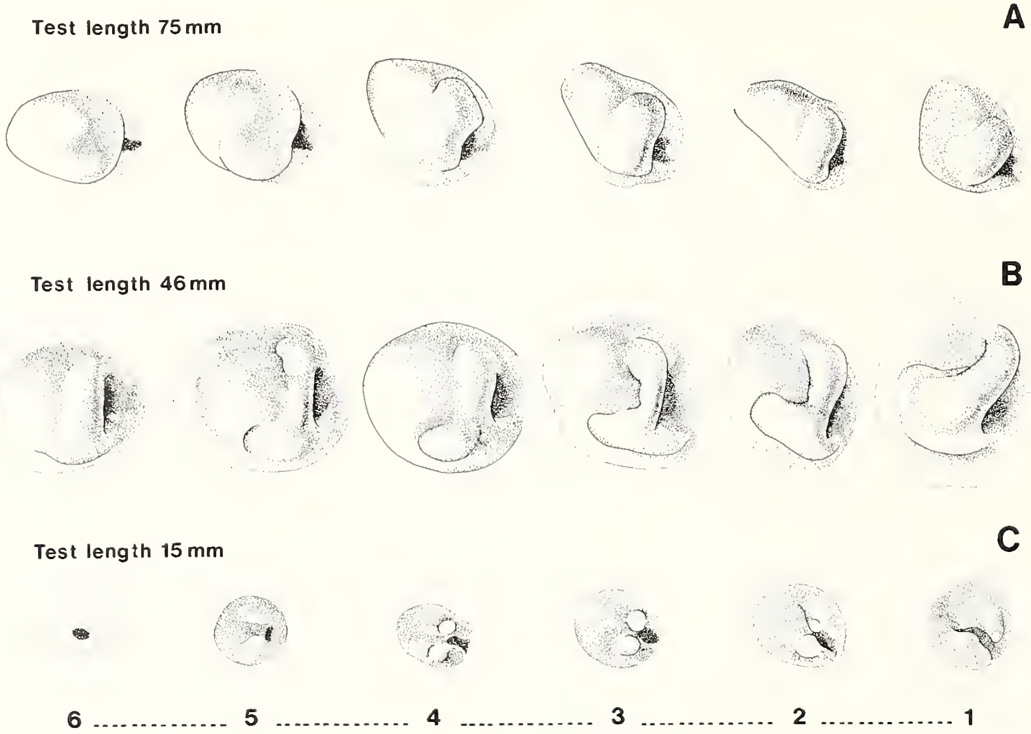
Material. Gray (1851, p. 133) described this species on the basis of 'several specimens' from Flinder's Island, Tasmania. Only three of these specimens can now be located. Two are numbered BMNH 60.12.17.4, of which that of intermediate size (maximum test length 58.8 mm) is herein chosen as the lectotype, and the third is BMNH 62.1.8.33.

The species is not common in collections. This description is based on eleven BMNH specimens: 72.6.22.25–27, 60.12.17.4 (two specimens), 62.1.8.33, 49.11.19.1, 1953.2.6.311–313, and one unregistered specimen; five TM specimens: H917–920, 15409/H70; sixteen WAM specimens: 397-74, 543-39, 276-74, 331-74 (two specimens), 122-37, 1770-74, 181-37, 41-44, 9491, 151-32, 152-32, 679-71, 740-83, and two unregistered specimens; and three UWA specimens: 41232.

In Tasmania it has been found off Flinder's Island and Cape Barren Island. It ranges as far north as Port Jackson in New South Wales. Clark (1946, p. 364) recorded it from Western Port, Victoria and Cotton and Godfrey (1942) recorded it from waters off South Australia. It occurs in south-western Australia from Hopetoun to as far north as Trigg Beach, Perth. Three specimens (UWA 41232) are known from the late Pleistocene Tamala Limestone, just south of the mouth of the Greenough River.

Description. Test ginger-coloured with prominent, large, black pedicellariae on aboral surface; reaches a maximum known length of 94 mm; widest anterior of centre in small specimen (15 mm TL), but widest posterior of centre in large specimens (75 mm TL); width 81–90% TL. Test highest at about mid-test length in interambulacrum 5; forms a weakly developed keel; height variable, 57–68% TL. Test has broad, shallow anterior notch in adult specimens (Pl. 32, fig. 7). Apical system ethmolytic, slightly depressed, with four genital pores; at 15 mm TL genital pores not open; at 28.5 mm TL genital pores open; situated 25–38% TL from anterior ambitus; migrates anteriorly with growth of test (text-fig. 3A).

Aborally ambulacrum III shallow, deepening abapically; bears isopores which are separated by prominent interporal partition; isopores increase in number from sixteen in juvenile specimen to twenty-seven in adults, and bear extensile tube feet tipped by light sensitive terminal pads (McNamara, 1984*b*). Anterior petals aligned transversely; anteriorly flexed distally. Petals 37–46% TL long, 6.5% TL wide; relatively shorter in smaller specimens (text-fig. 3D); each row bearing up to forty-one conjugate pore pairs; only twenty present in specimen 15 mm TL; number of pore pairs increases to about thirty-eight to forty-one in adults of about 50 mm TL, thereafter remaining constant in number with growth of test (text-fig. 3C). Rarely, poriferous plates in ambulacrum II or IV may be occluded. Posterior petals slightly shorter than anterior petals, 32–44% TL in

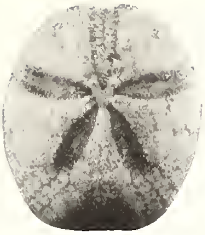


TEXT-FIG. 1. *Protenaster australis* (Gray, 1851); camera lucida drawings of phyllodal plates 1 to 6 of ambulacrum Ib. A, WAM 493-84, large adult with platform periporal area, × 15. B, WAM 151-32, small adult with reniform periporal area, × 30. C, WAM 397-74, juvenile with breached periporal area, × 33.

EXPLANATION OF PLATE 32

Figs. 1–8. *Protenaster australis* (Gray, 1851). 1–4, WAM 397-74, juvenile test, collected from reef platform, Cape Vlaming, Rottnest Island, Western Australia; wet specimen showing plate boundaries, ×2. 5, 6, WAM 331-74, from Bunker Bay, Western Australia, ×2. 7, 8, WAM 740-83, from sand pocket on limestone reef 30 m off Trigg Beach, Perth, Western Australia, buried 10 cm in 1.8 m of water, ×1.

All Recent. Figs. 5–8 whitened with ammonium chloride.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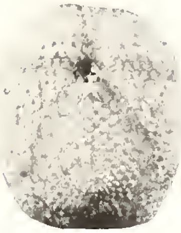
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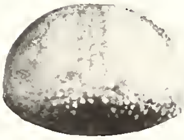
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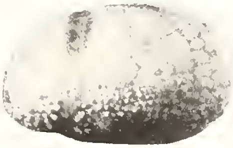
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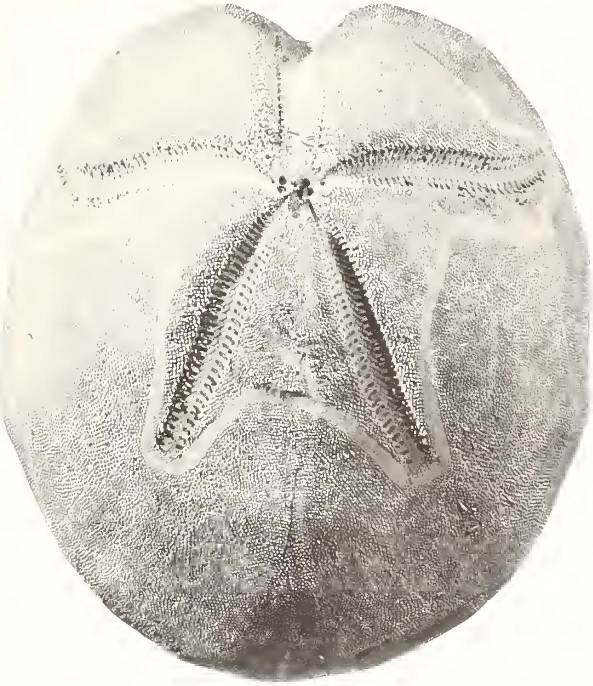
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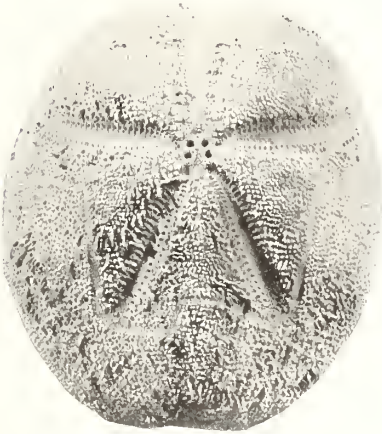
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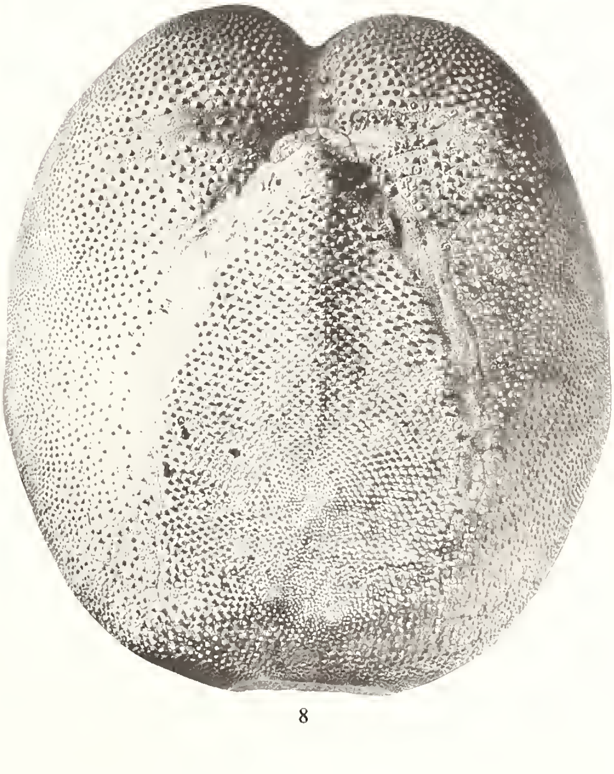
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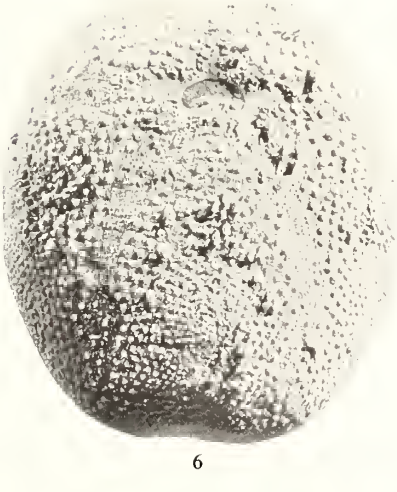
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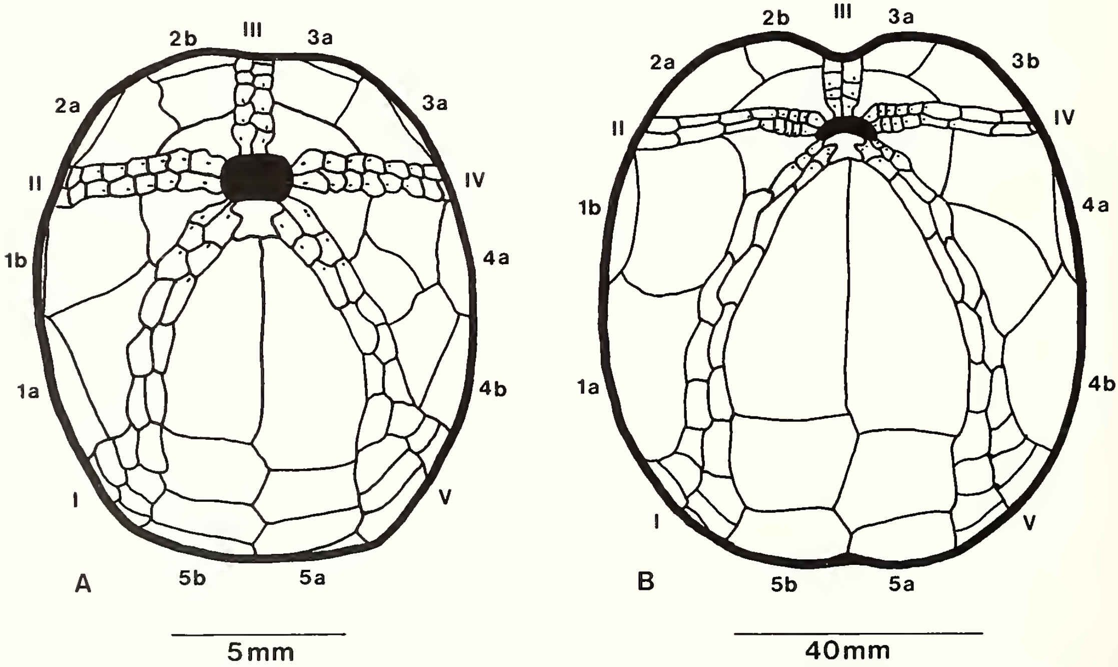
McNAMARA, *Protenaster*

adults, more so in juvenile; diverge at about 45–50°; each row bears up to forty-two conjugate pore pairs; rate of increase of number of pore pairs the same as for anterior petals. Peripetalous fasciole indented between petals; crosses interambulacra 1b/4b in plate 6, crosses plates 5–7 in 1a/4a, and plate 4 in 2a/3a and 2b/3b. Lateroanal fasciole one third width of peripetalous; crosses plate 5 of 1b/4b and plate 4 of 1a/4a.

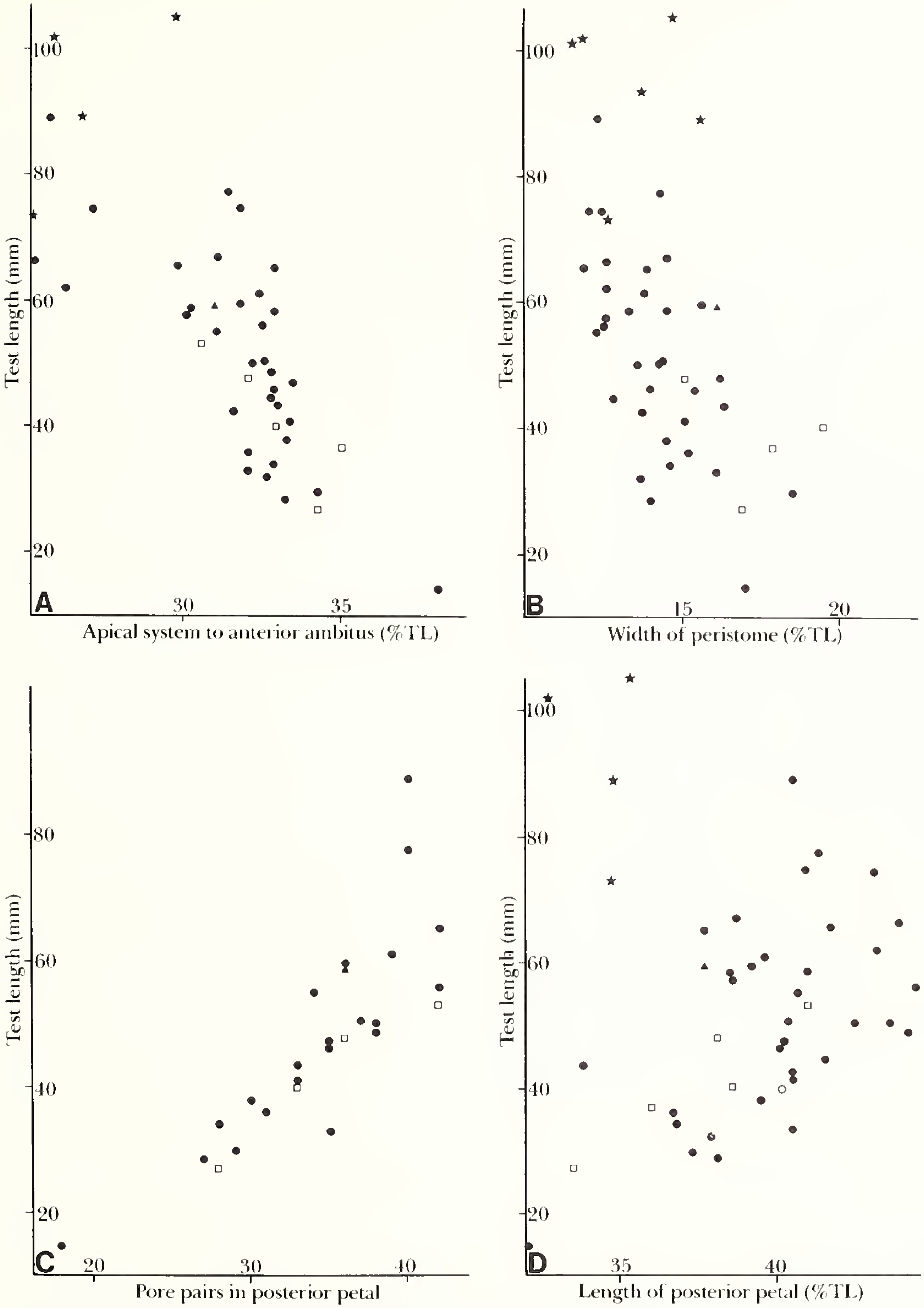
Peristome slightly sunken, lunate, width 12–19% TL, high values in small specimens; relative width progressively decreases with growth of test (text-fig. 3B). Anterior of peristome situated 22% TL from anterior ambitus in juvenile specimen, decreasing to 15% TL in large adults. With test growth labrum increasingly projects across peristome, reaching halfway in largest specimens (Pl. 32, fig. 8). Pores in phyllode generally unipores: eight pores in ambulacra I/V, twelve to fourteen in ambulacra II/IV, and seven or eight in ambulacrum III. With growth of the test, phyllodes pass through breached to platform stages of development. In juvenile specimen (15 mm TL) periporal area in breached condition (text-fig. 1C), apart from one plate which has isopores and a bridged interporal partition. In moderate sized specimens periporal areas have a reniform ridge (text-fig. 1B). In largest tests the abaxial part of the periporal area swells to form a raised platform (text-fig. 1A), which is separated from reniform ridge by a depression in which, rarely, a pore develops connecting to the main unipore.

Plastron broad but variable, 35–50% TL. Adoral plate 2 of interambulacrum 1b bisects plate 1 and plate 2 of interambulacrum 1a (text-fig. 2B) in all specimens examined, except the juvenile, where it fails to bisect and meet ambulacrum I (text-fig. 2A). Periproct oval, width about two-thirds length; length same as peristome width. Twenty-four tubercles per $5\ \text{mm}^2$ in interambulacrum 2 close to peristome in test 45 mm TL; twenty-one tubercles per $5\ \text{mm}^2$ in test 58 mm TL. Pedicellariae described in detail by Clark (1938) and Mortensen (1951).

Habitat. Hall (1904) recorded *P. australis* from a depth of 6 fathoms. One specimen in the WAM collection records the depth of collection of the live test as 25 fathoms. Recently McNamara and Bryce (1983) have described the habitat of the species off Trigg Beach, Western Australia. Two specimens were collected alive from sand where they were buried to a depth of 10 cm in water only 1.8 m deep, and only some 30 m offshore in a



TEXT-FIG. 2. *Protenaster australis* (Gray, 1851); adoral plating. A, WAM 397-74, juvenile, 15 mm TL, showing how the second plate of interambulacrum 1b fails to breach plates 1 and 2 of interambulacrum 1a. B, WAM 740-83, large adult, 90 mm TL, showing breaching of interambulacrum 1a by second plate of interambulacrum 1b.



TEXT-FIG. 3. Morphological changes during ontogeny of *Protenaster australis* (Gray, 1851) (●), *P. antiaustralis* (Tate, 1885) (▲), *P. preaustralis* sp. nov. (□), and *P. philipi* sp. nov. (★). Plots of test length against: A, distance of apical system from anterior ambitus (% TL); B, width of peristome (% TL); C, number of pore pairs in each row of the posterior petals; D, length of the posterior petals (% TL).

sheltered sand pocket on a limestone reef. Locality data with museum specimens suggests that this habitat may not be unusual for the species, as many specimens are recorded as having been collected from reef platforms or from beaches off which limestone reefs occur. Three further specimens were collected alive from the same sand pocket in January 1984. The sand is a fine-grained calcarenite (see McNamara and Bryce 1983, table 1, for grain-size analysis).

Remarks. Clark (1938) suggested that specimens collected from south-western Australia may belong to a different species from that occurring in Victorian and Tasmanian waters, because there appear to be some colour differences: a few Tasmanian bare tests have a purple tinge, a feature not seen in the south-western Australian specimens. This feature is not consistent and hardly seems a character worthy of specific differentiation. A small number of Tasmanian specimens examined do, however, show a greater degree of variation in certain morphological characters than the south-western Australian specimens. This variation is attributable to the paedomorphic nature of certain characters. For instance, two specimens (TM H918 and H920) both possess relatively shorter petals than other specimens of *P. australis*. However, this slight variation is not sufficient to warrant specific separation of the specimens. They merely lie at the extreme range of variation of the character, resembling juveniles of apaedomorphs.

The late Pleistocene specimens from south of the mouth of the Greenough River, Western Australia compare closely with living specimens in all characters except one: they possess slightly wider tests (90–92% TL, compared with 81.4–90% TL in living specimens). Again, they are merely considered to be variants lying at the extreme range of variation in this one character. The occurrence of these late Pleistocene specimens farther north than the present range of the species (29° latitude, compared with 32°) may indicate a more northward spread of the cold Western Australian current up the coast of Western Australia at some time during the last interglacial.

During the ontogeny of *P. australis* a number of morphological characters change allometrically. The widest part of the test migrates posteriorly during growth; the anterior notch is hardly present in the juvenile, but deepens during ontogeny; pore pairs in the aboral ambulacra increase in number to a test length of about 50 mm (text-fig. 3C); the anterior and posterior petals lengthen relatively during ontogeny (text-fig. 3D); the peristome decreases in relative width and the periproct decreases in relative length (text-fig. 3B); the peristome migrates anteriorly; the labrum lengthens; the pores in the phyllode pass through the breached, reniform, and platform stages; and the second adoral plate of interambulacrum 1b fails to bisect the first and second plates of interambulacrum 1a in the juvenile specimen, although it does in adults.

Protenaster antiaustralis (Tate, 1885)

Plate 33, figs. 1, 2, 5; text-fig. 4

1885 *Linthia antiaustralis* Tate, pp. 4–5.
1908 *Linthia antiaustralis* Tate; Chapman, pp. 215–216, pl. 19.
1908 *Linthia antiaustralis* Tate; Pritchard, pp. 397–398.
1946 *Linthia antiaustralis* Tate; Clark, pp. 365–366.

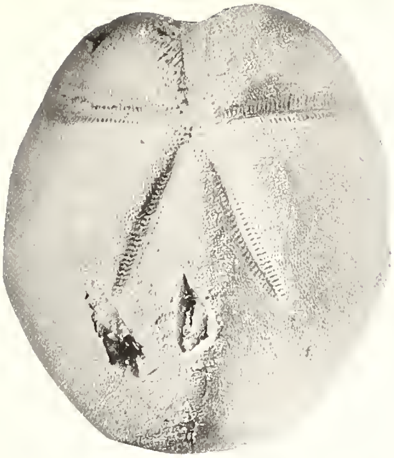
EXPLANATION OF PLATE 33

Figs. 1, 2, 5. *Protenaster antiaustralis* (Tate, 1885). SAM T268, holotype, from River Murray Cliffs, near Morgan, South Australia; Morgan Limestone (early Miocene), × 1.

Figs. 3, 4. *Protenaster australis* (Gray, 1851). 3, WAM 397-74, locality as for Plate 32, figs. 7, 8, × 1. 4, WAM 493-84, from Hopetoun, Western Australia, showing detail of the peristome and phyllode, with platform periporal areas, × 2.

Figs. 6–8. *Protenaster preaustralis* sp. nov. 6, SAM P24520 from Maslin Beach–Port Willunga district, South Australia; Tortachilla Limestone (late Eocene), × 1. 7, 8, SAM P24519, holotype, from same locality and horizon as fig. 6, × 1.

PLATE 33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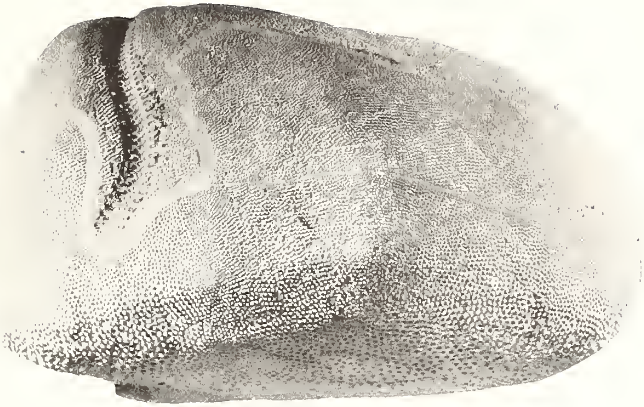
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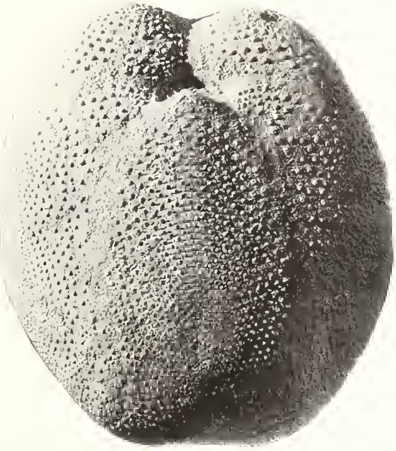
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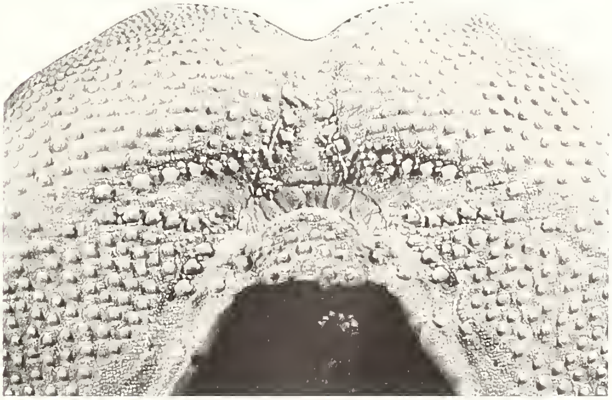
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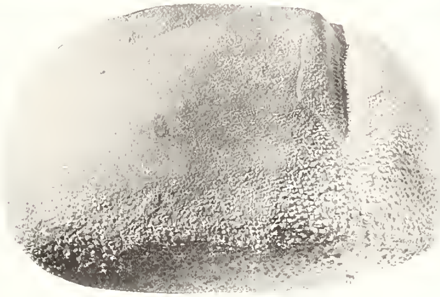
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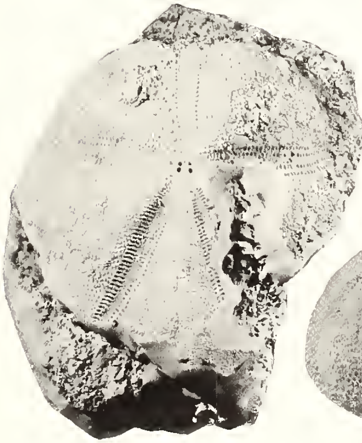
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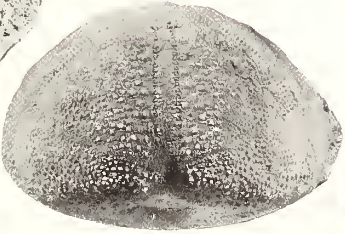
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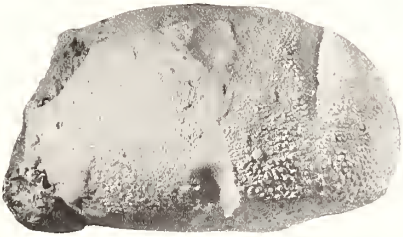
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McNAMARA, *Protenaster*

Diagnosis. Phyllodal pores unipores; periporal area breached in most plates, those closest to peristome reniform.

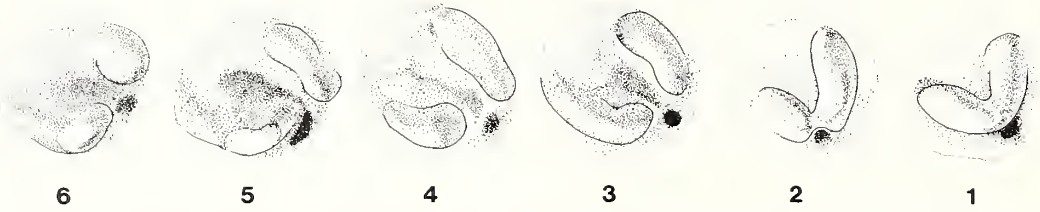
Material. The holotype, SAM T268, from the early Miocene 'calciferous sandrock' (probably the Balcombian Morgan Limestone), River Murray Cliffs, near Morgan, South Australia, and NMV P9154, from Balcombian strata at Curlewis, near Geelong, Victoria.

Description. Test up to 59 mm in length; widest posterior of centre, width 88% TL; highest at mid-test length in interambulacrum 5, which forms a keel (Pl. 33, fig. 5); height 66% TL; anteriorly a broad, shallow notch is present. Apical system ethmolytic, with four genital pores; situated 31% TL from anterior ambitus. Thirty isopores in ambulacrum III; each pore separated by prominent interporal partition. Anterior petals slightly anteriorly divergent at about 160°; almost straight, shallow, and bearing up to thirty-eight conjugate pore pairs in each row; length 38-43% TL. Posterior petals shorter than anterior pair, 35-38% TL; diverge at about 60°; bear up to thirty-six pore pairs in each row; slightly flexed distally (Pl. 33, fig. 1). Peripetalous and lateroanal fascioles follow same course as those in *P. australis.*

Peristome slightly sunken, lunate, width 16% TL. Anterior of peristome situated 17% TL from anterior ambitus. Labrum projects halfway across peristome (Pl. 33, fig. 2). Pores in phyllode are unipores; eight pores in ambulacra I, III, and V; twelve pores in ambulacrum II, thirteen in IV. Periporal area in plates 1 and 2 in ambulacra II and IV reniform; in plates 3-6 breached, degree of separation decreasing adaxially as raised segments lengthen (text-fig. 4). Similarly, periporal areas in first two plates of ambulacra I, III, and V reniform, others breached. Plastron quite broad, 40% TL. Plates 1 and 2 of interambulacrum 1a bisected by plate 2 of interambulacrum 1b. Periproct oval with long axis sagittal (16.5% TL) and width two-thirds length. Fourteen tubercles per 5 mm^2 in interambulacrum 2 close to peristome.

Remarks. Tate (1885, pp. 4-5) considered that *P. antiaustralis* differed significantly from *P. australis* in seven characters. However, analysis of the intraspecific variation of *P. australis* shows that four of these characters cannot be used to distinguish the species, highlighting the overall close morphological similarity between the living *P. australis* and the early Miocene *P. antiaustralis*; those which fall within the range of variation of *P. australis* are test height and width, the form of the adoral surface, and the size and depth of the apical system. However, three of the characters which Tate used to distinguish the two species are valid: *P. antiaustralis* has slightly shallower petals than *P. australis*; the difference in lengths of the anterior and posterior petals is more pronounced in *P. antiaustralis*; and the angle of divergence of the posterior petals is greater in *P. antiaustralis* (60°, not 50° as Tate stated). Furthermore, *P. antiaustralis* can be distinguished from *P. australis* by its relatively broader peristome (text-fig. 3B) and longer periproct; the presence of only breached and reniform periporal areas in the phyllode; and sparser tuberculation in interambulacrum 2 adorally.

Chapman (1908, pp. 215-216, pl. 19) illustrated a specimen which he assigned to *P. antiaustralis.* Pritchard (1908, pp. 397-398) was scathing in his criticism of Chapman's lack of description and poor illustration of the specimen. Furthermore, he doubted whether the two specimens were conspecific. However, examination of the specimen reveals that it does, indeed, belong in *P. antiaustralis.* Its relatively shorter petals are a function of its smaller size.



TEXT-FIG. 4. *Protenaster antiaustralis* (Tate, 1885); camera lucida drawings of phyllodal plates 1 to 6 of ambulacrum Ib. SAM T268, showing reniform periporal area in plates 1 and 2 and breached periporal areas in plates 3 to 6, the degree of breaching increasing away from the peristome, × 25.

Protenaster preaustralis sp. nov.

Plate 33, figs. 6–8; Plate 34, figs. 1–5; text-figs. 5, 6

Diagnosis. Phyllodal pores isopores. Second plate of interambulacrum 1b may or may not bisect plates of 1a adorally. Anterior notch weakly developed.

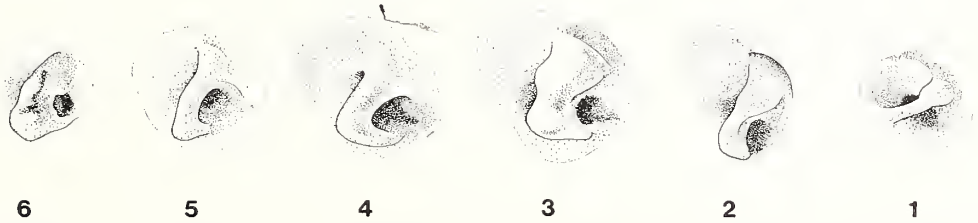
Material. Holotype SAM P24519, from the late Eocene Tortachilla Limestone, Maslin Beach–Port Willunga district, south of Adelaide, South Australia. Paratypes SAM P24520–24523 and NMV P71348, P71349, from same horizon and locality as the holotype. Another specimen WAM 66.577, from the Wilson Bluff Limestone (late Eocene), Nurina Cave (N46), Western Australia.

Description. Test up to 53 mm in length, widest slightly anterior of centre, width 87–91% TL; highest at mid-test length (Pl. 33, fig. 8); height 62–65% TL; anteriorly a very weak anterior notch is present (Pl. 33, fig. 6). Apical system slightly sunken; ethmolytic, with four genital pores; only just opened in smallest specimen (27 mm TL); situated 31–35% TL from anterior ambitus; closer to anterior in larger specimens (text-fig. 3A). Up to thirty isopores in a slightly sunken ambulacrum III; each pore separated by prominent interporal partition. Anterior petals slightly anteriorly divergent in smallest specimen (Pl. 34, fig. 1); transverse in larger specimens (Pl. 34, fig. 4); shallow and bearing up to forty-three pore pairs in each row; only thirty-three in smallest specimen; length 40–42% TL. Posterior petals shorter than anterior pair, length 34–41% TL; length increases relatively during increase in test length of 27–53 mm; diverge posteriorly at about 60%; pore pairs increase in number from twenty-eight to forty-two during known test growth; slightly flexed distally. Peripetalous fasciole not as indented between petals as in *P. australis*.

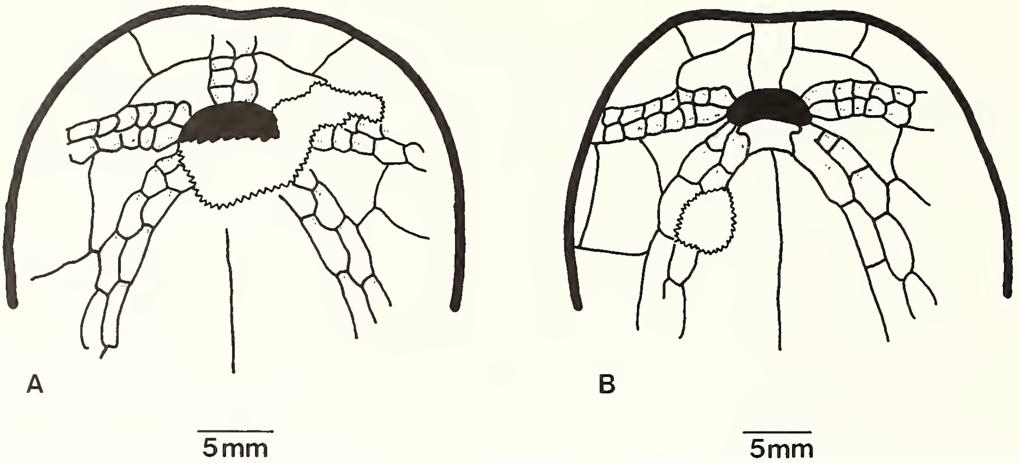
Peristome slightly sunken; width 15–20% TL. Labrum only known in smallest specimens, where it projects slightly across peristome (Pl. 34, fig. 2). Pores in phyllode are isopores, with bridged interporal partition (text-fig. 5): eight pore pairs in ambulacra I, III, V; twelve pairs in ambulacra II and IV. Plastron broad, 37–43% TL. Plates 1 and 2 of interambulacrum 1a bisected by plate 2 of interambulacrum 1b in three specimens (text-fig. 6B). In one specimen (SAM P24521), bisection does not occur (text-fig. 6A). Periproct oval, long axis slightly less than peristome width; periproct width two-thirds length. Sixteen tubercles per 5 mm^2 in interambulacrum 2, close to peristome, at 45 mm TL.

Remarks. The late Eocene *P. preaustralis* is very similar to the living species *P. australis*. It can be distinguished, however, by its possession of paired phyllodal pores; shallower anterior notch and ambulacrum III; shallow apical system; peripetalous fasciole which is less indented between the petals; and more sparsely distributed adoral interambulacral tuberculation in the anterior part of the test. Like *P. australis*, certain morphological characters in *P. preaustralis* change with growth of the test: the anterior notch becomes slightly deeper, the apical system moves forward, and the posterior petals lengthen at a greater rate than the anterior pair.

P. preaustralis can be distinguished from the early Miocene *P. antiaustralis* by its shallower anterior notch and ambulacrum III, more transverse anterior petals, a shallower apical system, a shallower peristome, and paired phyllodal pores. *P. preaustralis* is similar to *P. synapticus* from the late Eocene (Kaiatan) of New Zealand (Henderson 1975, pp. 20–21, pl. 2, figs. 7, 9–12). *P. preaustralis* can be distinguished, however, by its smaller peristome and less well developed keel in interambulacrum 5 aborally.



TEXT-FIG. 5. *Protenaster preaustralis* sp. nov.; camera lucida drawings of phyllodal plates 1 to 6 of ambulacrum Ib. SAM P24521, showing isopores and bridged periporal areas, × 30.



TEXT-FIG. 6. *Protenaster preaustralis* sp. nov.; adoral plating. A, SAM P24521, specimen showing failure of second plate of interambulacrum 1b to breach interambulacrum 1a. B, SAM P24522, specimen showing breaching of interambulacrum 1a by second plate of interambulacrum 1b.

Protenaster philipi sp. nov.

Plate 34, figs. 6, 7; text-fig. 7

Diagnosis. Moderately large species of *Protenaster* with a shallow anterior notch, and with short, narrow, deeply sunken petals. Phyllodal pores are unipores; raised periporal areas are generally breached.

Etymology. Named for Professor G. M. Philip, in honour of his work on Australian Tertiary echinoids.

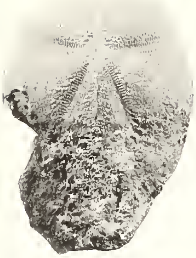
Material. Holotype MUGD 1690, from the Janjukian (late Oligocene) Waurn Ponds Limestone, Waurn Ponds, Victoria. Paratypes NMV P4776, P19990, P63040, P63059, and P63064, from the same locality and horizon as the holotype. Other material NMV P19989 and P78064 from the same locality and horizon as the holotype.

Description. Test sub-circular, moderately large, length up to 105 mm; widest at mid-length; width 91–97% TL; highest at mid-point in interambulacrum 5 posterior of apical system; height 57–60% TL. Apical system ethmolytic, with four genital pores; slightly sunken; anteriorly eccentric, situated 25–30% TL from anterior ambitus. Ambulacrum III sunken, but shallow; broad; leading to a broad, shallow anterior notch; bearing approximately twenty-seven small pore pairs, with pores in each pair aligned at about 45° and separated by raised interporal partition. Anterior petals diverging anteriorly at about 170°; wider and longer than posterior petals; length 41–43% TL; flexed anteriorly toward distal terminations, where they also shallow; deep adapically where they are overhung by anterior interambulacra; bearing approximately forty-five pore pairs; anterior and posterior rows separated by a distance equal to width of pore pairs, which are not sunken, nor conjugate. Posterior petals shorter than anterior pair (Pl. 34, fig. 6); length 35% TL; narrow, deeply sunken; diverging posteriorly at about 50°; like anterior petals, overhung by lateral interambulacra adapically;

EXPLANATION OF PLATE 34

Figs. 1–5. *Protenaster preaustralis* sp. nov. 1, 2, SAM P24522, × 1; 3, SAM P24521, × 1; 4, 5, SAM P24519, holotype, × 1. All from same locality and horizon as Plate 33, fig. 6.

Figs. 6, 7. *Protenaster philipi* sp. nov. MUGD 1690, holotype, from Waurn Ponds, Victoria; Waurn Ponds Limestone (late Oligocene), × 1.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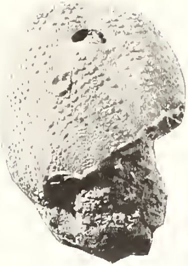
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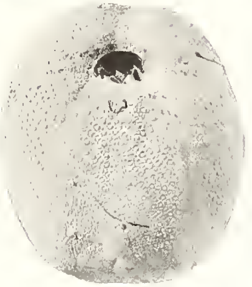
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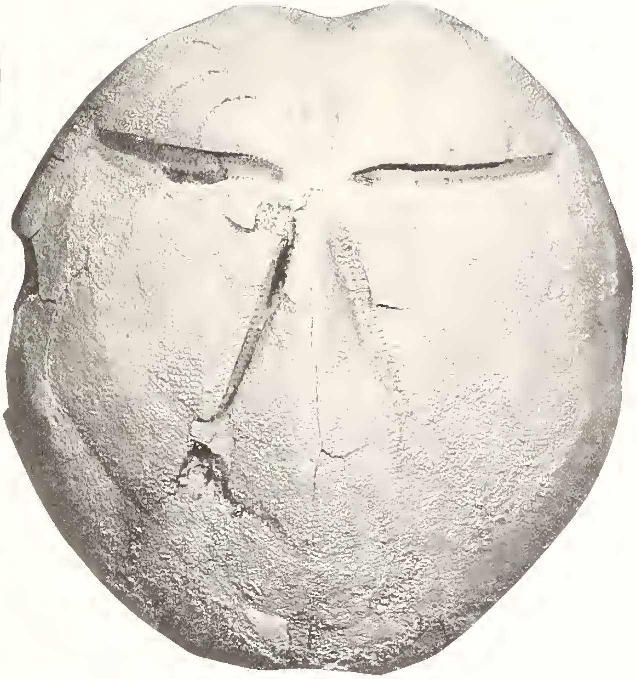
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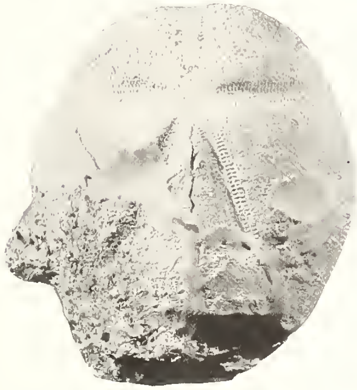
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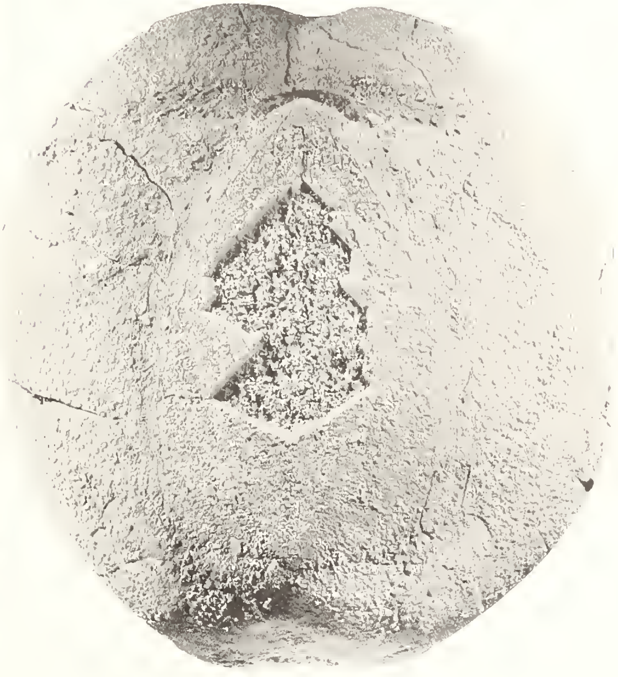
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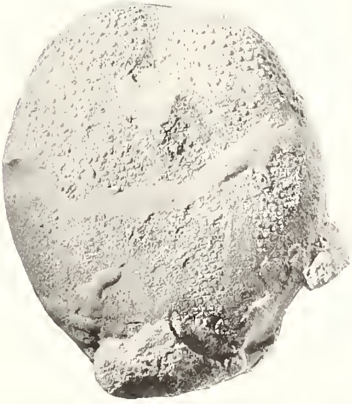
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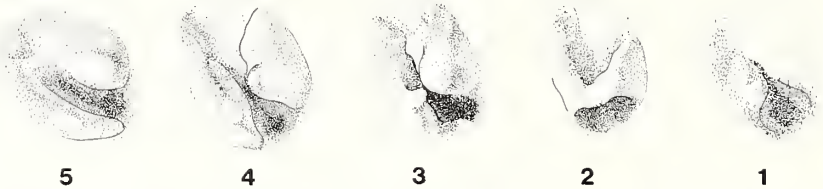
McNAMARA, *Protenaster*

shallowing distally. Peripetalous fasciole follows similar course to that of *P. australis* in lateral and posterior interambulacra; only slightly indented in anterior interambulacra, less so than in *P. australis*. Lateroanal fasciole narrower than peripetalous fasciole; meeting peripetalous fasciole close to distal extremity of anterior petal; extending 14% TL below periproct.

Peristome slightly sunken; situated anteriorly, only 9% TL from anterior ambitus; short and broad (Pl. 34, fig. 7), width 13-15% TL. Paratype NMV P63040 retaining two peristomial plates anteriorly: subrectangular, 3.5 mm in length. Labrum long; projecting almost entirely across peristome (Pl. 34, fig. 7). Phyllode with twelve or thirteen pores in ambulacra II and IV; six or seven in ambulacra I, III, and V; pores are unipores; periporal areas are raised and breached; closer to peristome extent of breaching reduced (text-fig. 7); occasionally plates closest to peristome may be reniform. Ambulacra slightly sunken adorally. Plastron large, width 44-47% TL. Second plate of interambulacrum 1b bisects first and second plates of interambulacrum Ia. Periproct oval, slightly sunken, 10-12% TL.



TEXT-FIG. 7. *Protenaster philipi* sp. nov. NMV P4776, camera lucida drawings of phyllodal plates 1 to 5 of ambulacrum Ib, showing breached periporal areas except for plate 2 in which a reniform plate has developed, × 15.

Remarks. The Janjukian strata at Waurn Ponds has been renowned for many years for the large spatangoids it has yielded. McCoy (1882) described *Pericosmus nelsoni* from the Waurn Ponds Limestone. This species has been placed in a number of genera by different workers, including *Linthia* and *Prenaster*. McNamara and Philip (1984) have recently placed it in a new genus, *Waurnia*. One of the reasons why *Pericosmus nelsoni* has at times been placed in *Linthia* (Pritchard 1908; Clark 1946; Gill 1952) is probably because of the coexistence, hitherto not recognized, of two species of spatangoids in the Waurn Ponds Limestone. The form described here as *Protenaster philipi* is, indeed, superficially similar to species of *Linthia*, but its near transverse anterior petals and bisected interambulacrum 1a adorally attest to its inclusion in *Protenaster*. It can be distinguished from the coexistent *W. nelsoni* by its deep petals and anterior notch.

P. philipi differs from other species of *Protenaster* in the shape of the test, which is less globose in form, and the nature of the interambulacra, which are flat, not convex, aborally. Furthermore, it has deeper, narrower petals than other species of *Protenaster*, and the posterior petals are relatively shorter.

EVOLUTION OF *PROTENASTER*

Peramorphic evolution of the phyllode

The five species of *Protenaster*, *P. preaustralis*, *P. synapticus*, *P. philipi*, *P. antiaustralis*, and *P. australis*, are remarkable for their morphological conservatism, the Eocene species closely resembling the later Tertiary ones, and these the living species. This phylogenetic conservatism is in marked contrast to the wide morphological variability displayed by a number of other Australian Tertiary spatangoids during their evolution, such as *Schizaster* (McNamara and Philip 1980), *Breynia* (McNamara 1982*b*), *Eupatagus* (Kruse and Philip, in press), and *Pericosmus* (McNamara and Philip 1984). The stable morphology of *Protenaster* is all the more remarkable when it is realized that the living species is such an extremely shallow water inhabitant (McNamara and Bryce 1983). All of the fossil species are preserved in bioclastic calcarenites (see below), suggesting that *Protenaster* has always been a shallow water inhabitant. *Protenaster* has undergone little change in its geographical distribution throughout the Tertiary, remaining confined essentially to southern Australia.

Selection pressure in genera such as *Schizaster* and *Pericosmus* was primarily centred on changes to the depths and lengths of the petals, anterior notch, size of the labrum, position of the apical system, and overall test shape. These changes have been interpreted as adaptations to the inhabitation of finer grained sediment (McNamara and Philip 1980, 1984). In *Protenaster* slight inter- and intraspecific variations occur in these characters, but much less than in other spatangoid genera. The morphological conservatism in *Protenaster* does not, however, apply to the structure of the phyllodal plates which surround the peristome. The pores and periporal areas undergo a large degree of morphological change during both the evolution of the genus and the ontogeny of later species. I consider that these changes also occurred in response to adaptation to a finer grained sediment (see below).

The tube feet of pores on phyllodal plates are highly specialized feeding structures in spatangoids, such as *Protenaster*. They bear a terminal cap which is covered by numerous, fine, mucous-secreting papillae. Such tube feet are termed penicillate tube feet and have the ability to pick up coarse to fine-grained sediment particles by mucous adhesion and pass them directly into the mouth. Elsewhere (McNamara, 1984*b*) it is shown that the phyllodal tube feet of *P. australis* are light-sensitive. Like the ambital sensory tube feet, the phyllodal tube feet undergo negative phototaxis at relatively low levels of ambient illumination. This is in contrast to the light-sensitive tube feet in the aboral ambulacrum III which undergo positive phototaxis at the same level of illumination. There is every reason to suppose that the fossil species also possessed this same facility to respond to light.

Protenaster compares with a number of Tertiary spatangoids in that during the course of its evolution the pores of the phyllode changed from being double to single pores. Kier (1974) demonstrated this change in species of *Linthia* and considered that in most spatangoids the change occurred during Palaeocene to Eocene times. McNamara and Philip (1980) described a similar change in *Schizaster*, species from the Tertiary of southern Australia demonstrating that the change occurred between the late Oligocene and early Miocene. The same change occurred in *Protenaster*, the late Eocene species *P. preaustralis* and *P. synapticus* having double pores, whereas the late Oligocene *P. philipi*, the early Miocene *P. antiaustralis*, and the Pleistocene to Recent *P. australis* have single pores in adults. As Kier (1974) and Smith (1980*a*) have pointed out, the double pores in the phyllode join below an interporal partition and only a single canal perforates the tests. The change from double to single pores in *Protenaster* occurred by breaching of the interporal partition sometime during the early to middle Oligocene; subsequently there occurred a sequence of changes to the form of the periporal area both during the ontogenetic and phylogenetic development of subsequent species. These changes may therefore be considered to have occurred by heterochrony. It will be argued that the heterochronic process was acceleration (*sensu* Alberch *et al.* 1979; McNamara, in press).

Increasing degrees of acceleration in the rate of development of the phyllodal plates through successive species in the Tertiary resulted in the development of a peramorphocline. A peramorphocline may be defined as a discontinuous morphological gradient of progressively more peramorphic species through time (McNamara 1982*a*). Successive species along the peramorphocline will pass through increasingly greater degrees of morphological change during their ontogenetic development. This peramorphic evolution (text-fig. 8) can best be illustrated in *Protenaster* by comparing the extent of phyllodal development in the extinct species with that of the living species; the phyllode of the latter passes through a greater number of morphological stages during its ontogeny than any of its ancestors; while the earliest species in the peramorphocline passed through the fewest.

The smallest specimen of the living species *P. australis* is a juvenile with a test length of 15 mm. Its phyllode possesses mainly unipores with the interporal partition in the breached condition (text-fig. 1c). In this character it therefore most closely resembles large adults of the late Oligocene *P. philipi*. On one plate of the juvenile *P. australis* isopores are present, the interporal partition having not been breached. This is the most 'primitive' condition and is found in adults of the Eocene species. With test growth, *P. australis* rapidly attains the reniform stage. Following the initial breaching of the interporal partition in the early juvenile stage, the residual stump decreases in size by resorption until the breach is about equal in width to the stumps. There then follows an adaxial migration and elongation of the stumps. Ultimately they rejoin to form a reniform ridge, the convex side of which is adaxially positioned and rises above the unipore (text-fig. 1B). Morphological change in the periporal area as it assumes a reniform shape must be accomplished by resorption of the stereom on the abaxial side of the stump, with subsequent regrowth on the adaxial surface. Various stages of this transformation can be identified in single specimens. This is because the plates closest to the peristome are relatively older than adapical plates. Thus the pore in plate 1 has longer to develop than the pore in plate 2, and so on. With such extensive ontogenetic morphological transformation as occurs in the phyllodal plates, the various stages may therefore be observed 'frozen' in a single specimen.

The reniform stage is attained in *P. australis* at a test length of about 30 mm. There is a certain degree of variation in rate of development of the phyllodal plates, and thus of attainment of the successive stages. This is illustrated by two specimens, each 30 mm in test length. One has all the phyllodal periporal areas in the reniform stage, while the other is more retarded in its development, the outermost plates still being in the breached condition. Between a test length of 30 mm and 50 mm, the rest of the plate, abaxial to the unipore and reniform ridge, swells. Thus by a test length of 60 mm most of the plates are in the platform stage, the whole plate forming a swollen, raised platform (text-fig. 1A). Swelling of the abaxial area continues in large specimens, such that at a test length of about 75 mm the central part of the periporal area may become slightly depressed. Occasionally a narrow channel may run from this depression and connect with the main unipore. Thus anisopores may, rarely, be present in these large specimens.

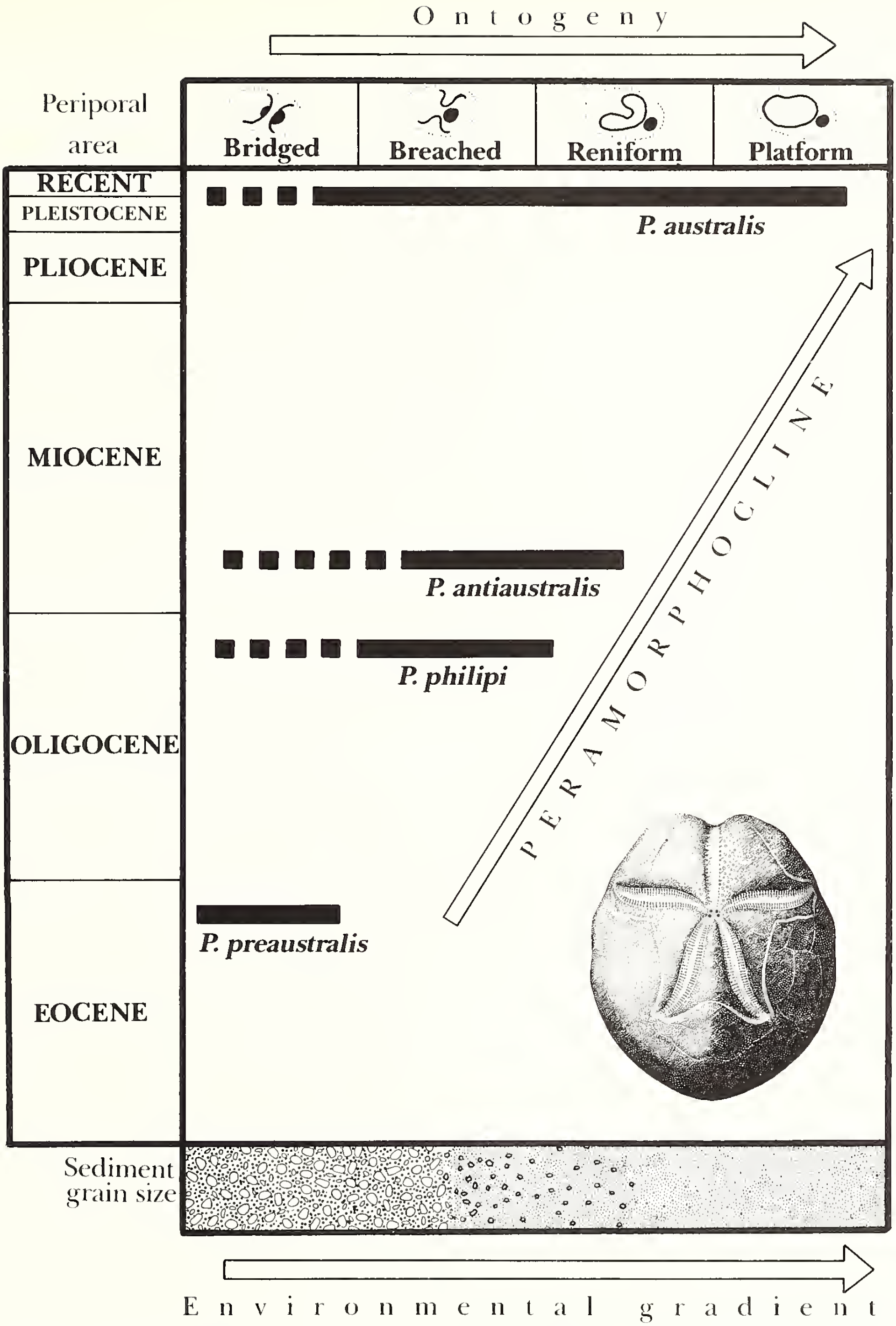
Whether or not the phyllode passes completely through all four stages of development is not known with certainty, as specimens smaller than 15 mm test length are unknown. There are two possibilities. Either the pores occur as isopores in early juveniles, with a bridged periporal area, or alternatively there has been pre-displacement (Alberch *et al.* 1979; McNamara, in press) and some plates commence development at a slightly more 'advanced' stage than in their ancestral species, perhaps beginning in the breached condition. However, the presence of one plate with bridged isopores in the juvenile specimen suggests that there may have been little or no pre-displacement.

Although it might be argued that the breached stage could be interpreted as a very early ontogenetic 'pre-bridged' phase, this is unlikely to be the case. If it were so the breached stage would be suceeded ontogenetically by the bridged stage. However, in all species the breached stage is succeeded by the reniform stage. This stage is quite distinct from the bridged stage in that the raised interporal partition develops on the periphery of the plate in an adaxial position, and not medially. Furthermore, in both the breached and reniform stages only a single pore perforates the test.

As described above, the late Eocene *P. preaustralis* and *P. synapticus* have phyllodal plates with bridged isopores. The next species, the late Oligocene *P. philipi*, is only known from large specimens, similar in size to the largest known specimens of *P. australis* which, at a similar size, have phyllodal plates in the platform stage. In *P. philipi* the periporal areas are nearly always in the breached condition. The extent of breaching is diminished closer to the peristome as the periporal areas are changing toward the reniform stage. This is only attained in two specimens of *P. philipi* in adoral plates. The early Miocene *P. antiaustralis* is slightly more advanced than *P. philipi* in that, although it is a smaller specimen than any known specimen of *P. philipi*, plates 1 and 2, close to the peristome, have attained the reniform stage. Plates 3 to 6 are breached, the degree of separation of the stumps increasing away from the peristome.

Functional significance of the phyllode peramorphocline

The phyllodal pores of *P. australis* bear penicillate tube feet. Observations on living specimens (McNamara and Bryce 1983; McNamara 1984*b*) have revealed that the tube feet in *P. australis*, as in other spatangoids, secrete mucus which allows the echinoid to pick up the fine calcarenite upon which it feeds, and pass it directly into the mouth. Golubic *et al.* (1975) have noted that calcarenite


O n t o g e n y
Periporal area
Bridged
Breached
Reniform
Platform
RECENT
PLEISTOCENE
PLIOCENE
MIOCENE
OLIGOCENE
EOCENE
P. australis
P. antiaustralis
P. philipi
P. preaustralis
PERAMORPHOCLINE
Sediment grain size
Environmental gradient

TEXT-FIG. 8. The evolution of the periporal areas of *Protenaster* in the Tertiary to Recent of southern Australia. Later species undergo progressively increased rate of development of this character by acceleration, resulting in the development of a peramorphocline which follows an environmental gradient of coarse to fine calcarenites. Inset, drawing of the aboral surface of *Protenaster australis* (Gray, 1851).

fragments are generally heavily bored by endoliths, such as algae and fungi. It is most probable that sediment ingesting organisms, such as *P. australis*, obtain much of their nutrition from this source.

McNamara and Bryce (1983) have documented the fine-grained nature of the sediment in which *P. australis* lives, about 75% of the grains being between only 0.125 mm and 0.25 mm in diameter. Examination of the enclosing lithologies of the fossil species has revealed that the earliest species inhabited the coarsest grained sediment, with later species inhabiting progressively finer-grained sediment (text-fig. 8). The late Eocene Tortachilla Limestone, in which *P. preaustralis* is preserved, is a poorly sorted, brown-green bryozoal calcarenite. Most sediment particles lie within the range 0.5–2 mm, with some up to 5 mm in diameter. The late Oligocene Waurn Ponds Limestone, in which *P. philipi* is preserved, is also a coarse bryozoal calcarenite of similar grain size to the Tortachilla Limestone. The calcarenite in which the early Miocene *P. antiaustralis* is preserved is finer grained, the sediment particles mainly lying in the range 0.2–0.5 mm, although some reach 1.5 mm in diameter. Smith (1980*b*, p. 43, fig. 109*b*) has observed that there is a general trend for the density of aboral turberculation in spatangoids to increase with decreasing sediment grain size. His observations are supported by *Protenaster* which shows an increase in tubercle density from sixteen per 5 mm^2 in the earliest species (the late Eocene *P. preaustralis*) to twenty-four per 5 mm^2 in the living *P. australis*.

Although it might be thought that the wide variety of phyllodal pores possessed by spatangoids would bear a wider range of penicillate tube feet, Smith (1980*a*) has shown that this is not the case. He has observed (Smith 1980*a*, p. 57) how the structure of phyllodal tube feet are remarkably uniform in holasteroids and spatangoids. Thus the pronounced change in phyllodal morphology in *Protenaster* is unlikely to reflect any change in the structure of the tube feet. However, during the evolution of *Protenaster* there appears to be a reasonably direct correlation between the transformation in the nature of the phyllodal plates and the changing sediment grain size, from coarse to fine calcarenite. This suggests that although there may not have been any great change in the structure of the tube foot, there may have been substantial changes to the mechanical ability of the tube foot to cope with sediments of different grain size.

Smith (1980*a*, p. 76) has observed that large periporal areas were developed in the phyllodes of many spatangoids to allow the stem of the tube foot to be wide enough to support the large papillate terminal disc. However, Smith could see little reason for the development of raised periporal areas, such as those in *P. australis*. He suggested the possibility that a domed periporal area may help to maintain coelomic fluid movement in the lumen by increasing the surface area of the single layer of squamous epithelium which covers the periporal area.

The trend in *Protenaster* is for the surface area of the periporal region to undergo a relative decrease, both ontogenetically and phylogenetically, as it transforms from the bridged to breached to reniform to platform conditions. It is possible that the larger surface area was necessary to allow the penicillate tube foot to pick up larger sediment particles. With a decrease in this surface area the tube foot may well have been restricted in the size of sediment particle which it could pick up. Preferential phylogenetic selection of this character was probably favoured because of the inability of most spatangoids, particularly those inhabiting shallow water, to inhabit fine-grained sediments.

The large morphological change of the phyllodal plates in *P. australis* during ontogeny suggests that juveniles may feed on coarser-grained sediment than adults. Examination of the gut contents of the small 15 mm long juvenile has confirmed this, the sediment being much coarser than sediment upon which the adults feed, lying in the range 0.3–1.0 mm diameter. The occupation by juvenile *P. australis* of coarser sediment than adults is also indirectly indicated by the lower concentration of adoral tuberculation in the 15 mm long specimen. The concentration is about as low as that in the earliest species of *Protenaster*, *P. preaustralis* and *P. synapticus*.

It is also conceivable that the change from isopores to unipores during the Tertiary, which has been recorded in other spatangoids (Kier 1974; McNamara and Philip 1980), also occurred in conjunction with adaptations to the inhabitation of finer-grained sediments. McNamara and Philip (1980) have shown that the morphological changes in the *Paraster–Schizaster* lineage also formed a peramorphocline which followed an environmental gradient of coarse to fine-grained sediment. One of these changes was the transformation of the phyllodal pores from isopores to unipores. The independent acquisition of phyllodal unipores in a number of spatangoid lineages may therefore be explained by selection of morphotypes capable of inhabiting and feeding upon finer-grained sediments.

Ontogenetic and phylogenetic development of the adoral plates of interambulacrum 1

One of the characteristics of *Protenaster* is the presence of an enlarged second plate of interambulacrum 1b which separates the first two plates of interambulacrum 1a (text-fig. 2B). This character is present in a number of other genera, including *Pericosmus*, *Paleopneustes*, *Faorina*, and *Plesiozonus*. Largely on the basis of this character Chesher (1968) argued that these four genera should be placed in a single family, the Paleopneustidae. However, McNamara (1984*a*) and McNamara and Philip (1984) have provided evidence of the strong intraspecific variation in the presence of this character. The analysis of this structure in *Protenaster* provides support for the contention that this character varies both ontogenetically and intraspecifically between adults, and is therefore unsuitable as a major familial character in spatangoids.

Although Chesher (1968) considered the enlarged plate to be a compound plate of the second plates of both 1a and 1b, the ontogenetic transformation of its structure in *P. australis* shows that the plate is not compound, but merely the enlarged second plate of interambulacrum 1b. This can be demonstrated by comparing the adoral plate arrangement of a juvenile and adult *P. australis*. In the juvenile the adoral plates of interambulacrum 1 are in a 'normal' condition, i.e. the second plate is in contact only with ambulacrum II (text-fig. 2A). In adults this plate abuts both ambulacra I and II. During growth of the test this plate expands to such an extent that it bisects the first and second plates of interambulacrum 1a. The changing nature of such adoral plate boundaries is currently being appraised (McNamara and Philip, in prep.).

Whereas the second plate of interambulacrum 1b is always in the expanded condition in adults of the living species *P. australis*, adults of the earliest species *P. preaustralis* have both conditions (text-fig. 6). Thus later species of *Protenaster* may be considered to have undergone an increase in the rate of allometric growth of this plate, such that only the expanded plate condition occurs in adults.

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THE MID-PROTEROZOIC LITTLE DAL MACROBIOTA, MACKENZIE MOUNTAINS, NORTH-WEST CANADA

by H. J. HOFMANN

ABSTRACT. The Little Dal macrobiota is now known to comprise the previously reported carbonaceous megafossils *Chuaria circularis*, *Tawuia dalensis*, *Morania*? *antiqua*, and *Beltina danai*, as well as the following additional taxa: *Longfengshania stipitata*, *Grypania spiralis*, *Daltaenia mackenziensis* n.g. and sp., *Tyrasotaenia* sp., and *Tyrasotaenia*? sp. The dubiofossil '*Bergaueria*?' reported earlier is probably nonbiogenic.

Of special interest are three-dimensionally preserved specimens of *Chauria*, *Tawuia*, and *Tyrasotaenia*?, found associated with 'molar-tooth' structure. A carbonized test separates the pure, equigranular, microcrystalline calcite infilling of the fossil interior from an argillaceous carbonate matrix. This infilling is optically and chemically indistinguishable from that comprising the 'molar-tooth' structure. These relationships indicate comparable processes and timing for both fossilization of the organisms and filling of syneresis cracks during compaction and consolidation of the sediment.

THE first elements of the Little Dal macrobiota were discovered and collected by J. D. Aitken in 1976 while mapping the Proterozoic succession in the Mackenzie Mountains for the Geological Survey of Canada. The collection was enlarged during the following year and a preliminary report on this important find was published (Hofmann and Aitken 1979). The Little Dal biota, particularly the association of *Chuaria* and *Tawuia*, has since been recognized in approximately coeval rocks elsewhere, at localities in China (Xing 1979; Zheng 1980; Du 1982; Duan 1982), Svalbard (Knoll 1982), the Vindhyan of India, and in a second formation of the Little Dal Group (for summary, see Hofmann 1985). There can be little doubt that macroscopic organisms of as yet undetermined, but most likely eucaryotic, algal affinities were widespread in rocks of 1·0–0·7 Ga age. As more occurrences come to light we may see a trend leading to the eventual recognition of a distinct chronostratigraphic interval typified by this macrobiota, just as there are now proposals for establishing an Ediacaran/Vendian Period and System characterized by a unique soft-bodied metazoan fauna (Jenkins 1981; Cloud and Glaessner 1982; Sokolov and Fedonkin 1984). With the oldest structured, macroscopic carbonaceous remains (filaments in the Changcheng System of China) dating back to about 1·8 Ga (Hofmann and Chen 1981), and the presence of a macrobiota in the approximately 1.3 Ga old Greyson Shale of Montana (Walter, *et al.* 1976), the whole interval of the middle and late Proterozoic becomes a more and more attractive target in the search for evidence of macroscopic life. The purpose of this paper is to furnish data on new material from the Little Dal Group collected since the initial account was published. The collections here reported come from two formations at five localities in the Mackenzie Mountains, as shown in text-figs. 1 and 2; two of the localities (1 and 2) had previously yielded specimens (Hofmann and Aitken 1979).

The large number of specimens now available from the Little Dal Group demonstrate a simple gross morphology of the two predominant taxa, but they also exhibit some unusual preservational variants (Pls. 35–38), including three-dimensionally preserved forms. The latter are associated with 'molar-tooth' structure, thin crumpled sheets of calcite which are a characteristic feature of certain Helikian (mid-Proterozoic) carbonate sequences of North America (see Smith 1968; O'Connor 1972; Donaldson 1973). The identical nature of the distinct equigranular microcrystalline calcite filling of both fossil and 'molar-tooth' structures is helpful in elucidating both taphonomic aspects and the diagenetic history of this type of carbonate sediment, as discussed further on.

[Palaeontology, Vol. 28, Part 2, 1985, pp. 331–354, pls. 35–39.]

GEOLOGIC SETTING

The stratigraphy and sedimentology of the Little Dal Group is treated at some length by Aitken (1981). The group is part of the Mackenzie Mountains Supergroup and comprises an Helikian epicratonic sequence of stromatolitic dolostones, mature clastics, and evaporites. The approximately 2 km thick succession overlies quartzites of the Katherine Group, and underlies a regional unconformity, above which are volcanics and cupriferous dolostones of the Redstone River and Coppercap Formations, referred to by Aitken as the 'Copper cycle'. The latter rocks are themselves unconformably overlain by the late Proterozoic Rapitan Group, which includes widespread glacigene deposits and an iron-formation. The whole assemblage is allochthonous, having been thrust north-eastward further on to the North American craton during the Laramide orogeny, much like a similar package comprising the Purcell and Windermere Supergroups in the southern Canadian Cordillera.

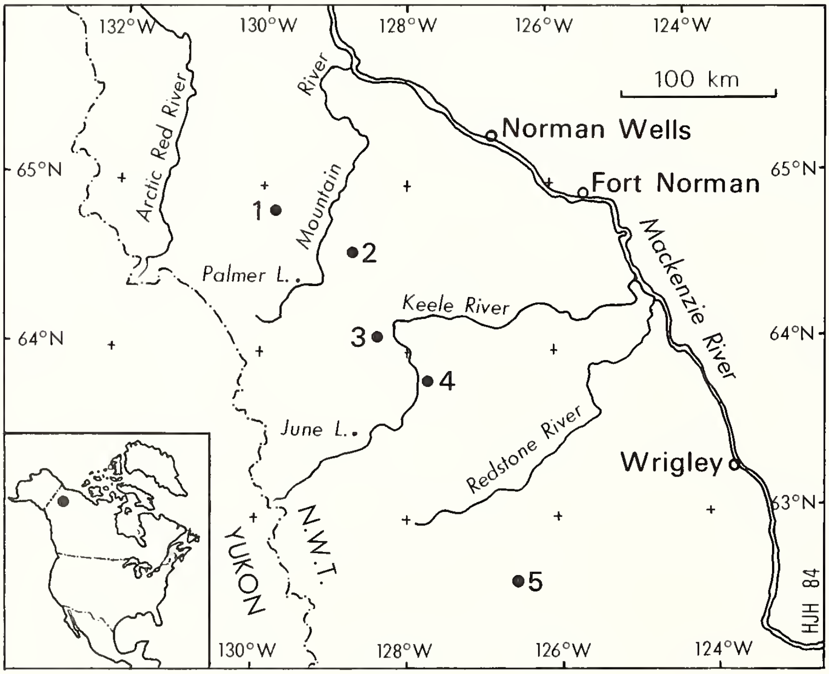
The Little Dal Group is divided into informally named lithostratigraphic units of formational rank, as shown in text-fig. 2, each reflecting a particular setting on the ancient craton. A regional multistage stromatolite buttress ('Rouge Mountain Member') in the lower part of the group separates a platform assemblage in the south-east from a basinal rhythmite assemblage in the north-western part of the area. The macrobiota is now known from both the basinal and the platform assemblages, as well as from the Rusty shale unit in the upper part of the group.

Locality details

The present study is based on new collections made by the writer at localities 1, 2, and 4, and on collections made by J. D. Aitken at localities 3 and 5. The localities are as follows:

Locality 1. 64° 48′ N. 129° 52.5′ W. (see Section 76AC-2 in Hofmann and Aitken 1979, figs. 1, 8; middle portion of Basinal assemblage).

Locality 2. 64° 37′ N. 128° 50′ W. (see Section 77AC-38 in Hofmann and Aitken 1979, figs. 1, 8; lower half of Basinal assemblage).



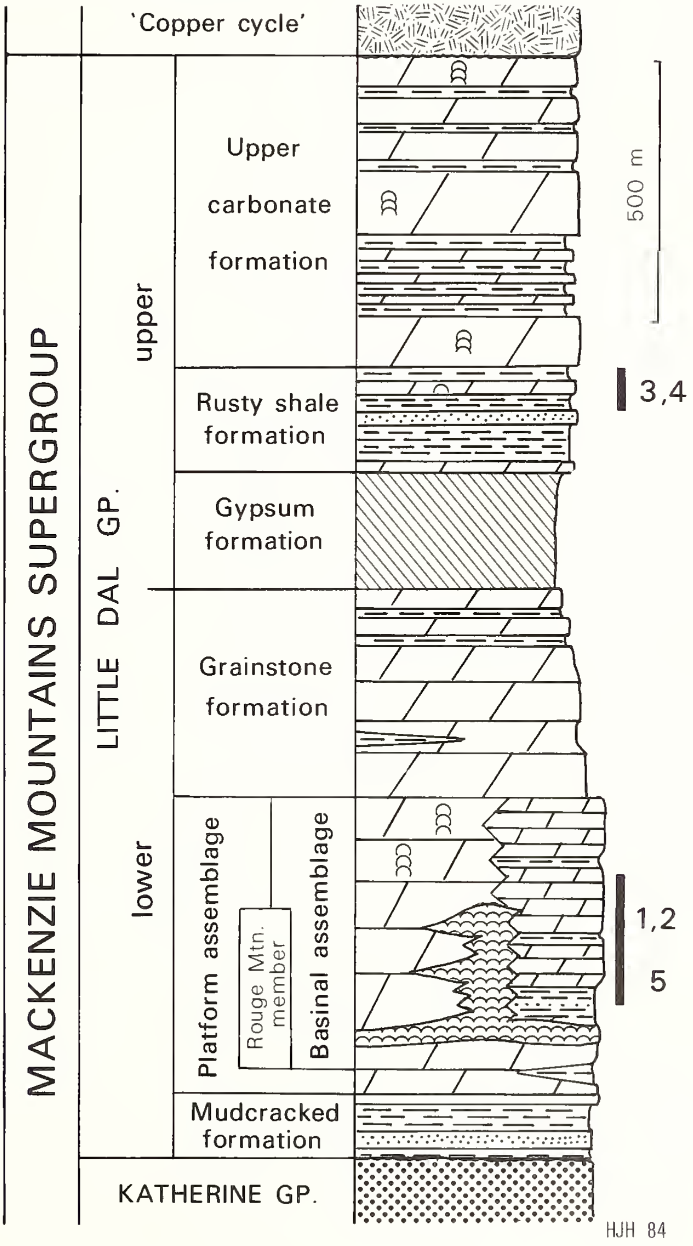
TEXT-FIG. 1. Map showing localities 1 to 5.

Locality 3. 64° 06′ 25″ N. 128° 27′ 30″ W. (see Section 77-36 in Aitken 1981, fig. 3.3, 3.17; Geol. Surv. Canada locality C85852, approximately 51·7 m below top of Rusty shale formation).

Locality 4. 63° 50′ 20″ N. 127° 33′ 55″ W., at an elevation of approximately 1170 m (see florencite locality illustrated photographically in Pouliot and Hofmann 1981; upper part of Rusty shale formation).

Locality 5. 62° 37′ 31″ N. 126° 36′ 40″ W. (see Section 79-2 in Aitken 1981, fig. 3.3, 3.12; Geol. Surv. Canada locality C85853, Platform assemblage, interval 238·3–260·5 m above base of section; in type section of Little Dal Group).

All specimens illustrated are deposited in the National Type-fossil Collection, Geological Survey of Canada, Ottawa, under the GSC accession numbers cited in each plate caption.


'Copper cycle'
MACKENZIE MOUNTAINS SUPERGROUP
LITTLE DAL GP.
upper
lower
Upper carbonate formation
Rusty shale formation
Gypsum formation
Grainstone formation
Platform assemblage
Rouge Mtn. member
Basinal assemblage
Mudcracked formation
KATHERINE GP.
500 m
3,4
1,2
5
HJH 84

TEXT-FIG. 2. Generalized stratigraphic column for Little Dal Group (after Aitken 1981), showing two intervals with megafossils (vertical bar) and collecting localities 1 to 5.

SYSTEMATIC PALAEONTOLOGY

In the following section, full synonymies are not presented for each species. Instead, the reader is referred to recent papers citing synonymies.

As presently construed the Little Dal macrobiota comprises the following taxa:

INCERTAE SEDIS
  Algae?
    Tawuia dalensis Hofmann, 1979
    Chuaria circularis Walcott, 1899
    Longfengshania stipitata Du, 1982
    Morania? *antiqua* Fenton and Fenton, 1939
    Beltina danai Walcott, 1899
    Daltaenia mackenziensis Hofmann, gen. et sp. nov.
    Grypania spiralis Walter, Oehler and Oehler, 1976
    Tyrasotaenia sp.
    Tyrasotaenia? sp.

DUBIOFOSSILS, probably nonbiogenic
  '*Bergaueria*?' Hofmann, in Hofmann and Aitken, 1979

Genus TAWUIA Hofmann, in Hofmann and Aitken, 1979

Type species. Tawuia dalensis Hofmann, in Hofmann and Aitken, 1979.

Tawuia dalensis Hofmann, in Hofmann and Aitken, 1979

Plate 35, figs. 1–3; Plate 36, figs. 1–5, 7–11; Plate 37, figs. 1, 2, 4–7; Plate 38, figs. 1–3; text-figs. 3, 4 (partim).

1977 *Fermoria* with 'filament', Sahni, pp. 293, 298.
1979 *Tawuia dalensis* Hofmann, in Hofmann and Aitken, pp. 157–160, figs. 13, 15, 16.
1979 *Shouhsienia shouhsienensis* Xing, p. 12, pl. 12, figs. 6–7 (nom. nud.).
1979 ?*Shouhsienia longa* Xing, p. 12, pl. 15, fig. 5 (nom. nud.).
1979 *Vendotaenia* sp. Xing, p. 12, pl. 12, fig. 9 (non 8).

EXPLANATION OF PLATE 35

Carbonaceous compressions and three-dimensionally preserved specimens of *Tawuia dalensis* Hofmann, *Chuaria circularis* Walcott, *Tyrasotaenia* sp., and *Tyrasotaenia*? sp., all from locality 1.

Specimens in figs. 4, 8–10 from slab illustrated in text-fig. 4.

Fig. 1. Bedding surface showing highest observed concentration of carbonaceous compressions of *Tawuia dalensis* Hofmann. GSC 77176, × 1.

Fig. 2. Association of *T. dalensis* Hofmann containing submillimetric discs, and *C. circularis* Walcott. Straight specimen at top is enlarged in fig. 6. GSC 77177, × 1.

Fig. 3. Specimen of *T. dalensis* Hofmann with concentric terminal folds, most likely due to compaction. GSC 77178, × 2.

Fig. 4. Three-dimensionally preserved specimens of *C. circularis* Walcott with surface indentations due to compaction, and nearby *Tyrasotaenia*? sp. GSC 77179, × 10.

Fig. 5. Bedding surface showing dense population of *C. circularis* Walcott and short specimens of *Tawuia dalensis* Hofmann with axial marking. GSC 77191, × 1.

Fig. 6. Enlarged view of specimen at top of fig. 2, showing large number of submillimetric discs. GSC 77177, × 4.

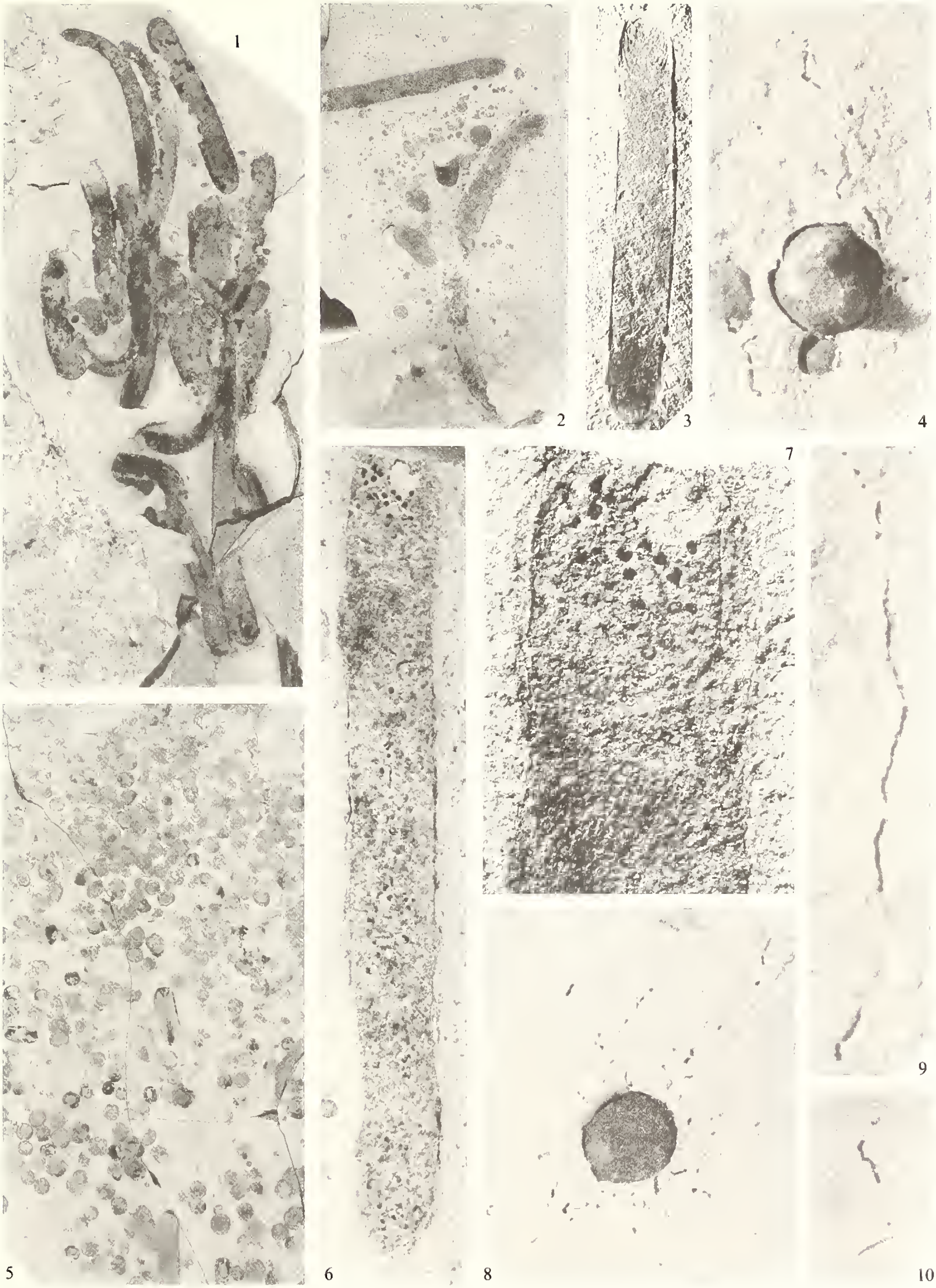
Fig. 7. Enlarged view of submillimetric discs in fig. 6. × 10.

Fig. 8. Three-dimensionally preserved *C. circularis* with subradially oriented *Tyrasotaenia*? sp. GSC 77180, × 10.

Fig. 9. Three-dimensionally preserved *Tyrasotaenia*? sp. GSC 77181, × 10.

Fig. 10. Carbonaceous compressions of *Tyrasotaenia* sp. on same slab as fig. 9. GSC 77182, × 10.

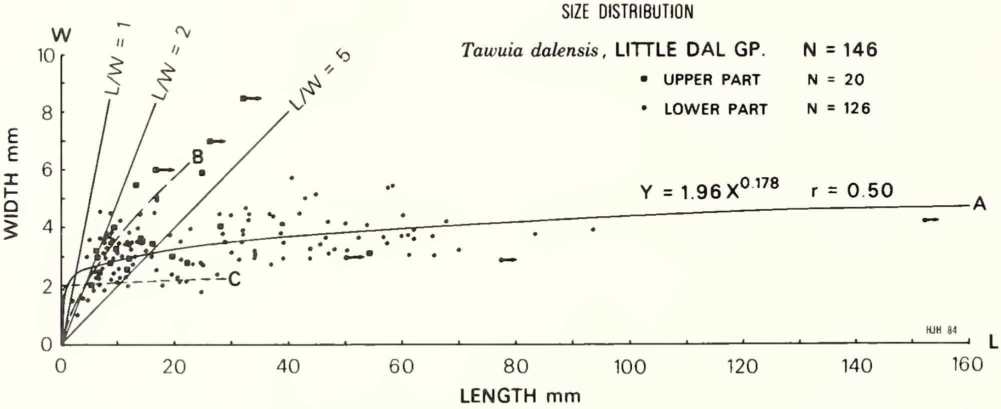
PLATE 35


1
2
3
4
5
6
7
8
9
10

HOFMANN, *mid-Proterozoic macrofossils*

1980 *Tawuia* cf. *dalensis* Zheng, in Yang *et al.*, p. 254, pl. 17, fig. 29.
1980 *Tawuia* cf. *dalensis* Zheng, p. 64, pl. 2, fig. 29.
1980 *Tawuia striatis* Zheng, in Yang *et al.*, p. 254, pl. 17, fig. 28 (nom. nud.).
1980 *Tawuia striatia* Zheng, pp. 63, 64, pl. 2, fig. 28.
1980 *Tawuia* spp. Zheng in Yang *et al.*, p. 254, pl. 17, figs. 24–27.
1980 *Tawuia* spp. Zheng, pl. 2, figs. 24–27.
1980 *Ellipsophysa axicula* Zheng, in Yang *et al.*, p. 253, pl. 17, figs. 5, 6 (nom. nud.).
1980 *Ellipsophysa axicula* Zheng, p. 60, pl. 1, figs. 5, 6.
1980 *Ellipsophysa proceriaxis* Zheng, in Yang *et al.*, p. 254, pl. 17, figs. 11, 13, 15, (nom. nud.).
1980 *Ellipsophysa proceriaxis* Zheng, p. 60, pl. 1, figs. 7, 13; pl. 2, figs. 11, 15.
1980 *Pumilibaxa huaihoiana* Zheng, in Yang *et al.*, p. 254, pl. 17, figs. 9, 12, 32 (nom. nud.).
1980 *Pumilibaxa huaiheiana* Zheng, p. 62, pl. 1, fig. 9.
1980 *Nephroformia liulaopeiensis* Zheng, in Yang *et al.*, p. 254, pl. 17, fig. 31 (nom. nud.).
1980 *Nephroformia liulaobeiensis* Zheng, pp. 62–63, pl. 1, fig. 31.
1982 *Shouhsienia shouhsienensis* Du (partim), p. 3, figs. 6, 10.
1982 *Shouhsien longa* Du, p. 3, fig. 9 (nom. null.).
1982 *Tawuia dalensis* Duan, p. 63, fig. 5K–N.
1982 *Tawuia sinensis* Duan, pp. 63–64, figs. 3K–Q, 5P(partim), 6.
1982 *Tawuia dalensis* Knoll, p. 275, text-fig. 3; pl. 3, figs. 13, 14.
1985 *Tawuia dalensis* Hofmann, fig. 4.

Description. Taxon characterized by straight and curved, roundly terminated tomaculate (sausage-shaped) objects, 1–8.5 mm wide (mean width = 3·42 mm; σ = 1·03 mm; N = 146), and generally several centimetres long (mean length = 25·44 mm; σ = 22·30 mm; N = 146), mostly with an aspect ratio (length/width) between 2 and 5 (text-fig. 3), the longest specimen (incomplete) with a length of 15·2 cm (Pl. 38, fig. 1). The specimens isolated as well as clustered, closely associated with abundant *Chuaria*, both preserved either as lustrous black or greenish carbonaceous compressions, as impressions if carbonaceous film absent, and, rarely, as three-dimensional objects. The outline generally smooth and even, although various kinds of folds may be present; the sides parallel to slightly tapering in short individuals, termini hemispherical or semicircular, rarely slightly pointed. In some specimens a disc-like terminal structure visible (Pl. 35, fig. 3; Pl. 36, figs. 1, 11), while in others a



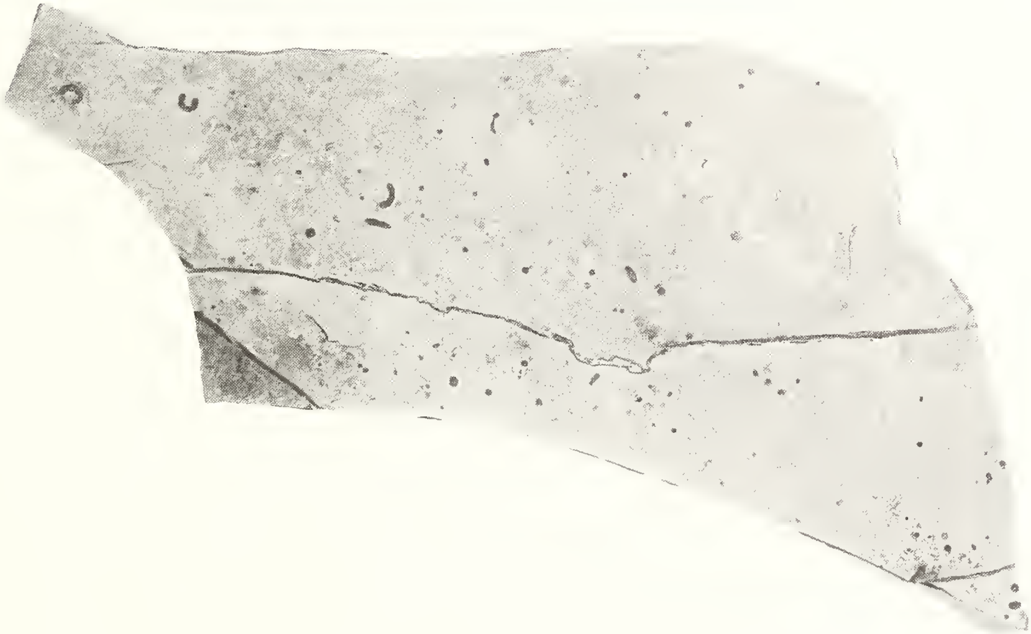
TEXT-FIG. 3. Bivariate plot of size distribution of *Tawuia dalensis* Hofmann in Little Dal Group. Points with arrows indicate minimum lengths of incomplete specimens. Compilation includes the eighteen data points reported by Hofmann and Aitken (1979, fig. 15). Geometric regression lines added for comparison; A, *T. dalensis*, Little Dal Group; B, *T. dalensis*, Kapp Lord Farm, $Y = 0{\cdot}73X^{0{\cdot}692}$, $N = 125$ (Knoll 1982, text-fig. 3); C, *T. sinensis* Duan, Liulaobei Farm, $Y = 1{\cdot}97X^{0{\cdot}035}$, $N = 33$, $r = 0{\cdot}08$ (Duan 1982, text-fig. 6). Aspect ratio lines (L/W) are also plotted to show concentration of specimens in region with L/W between 2 and 5.

dark axial or off-axial zone present (Pl. 35, fig. 5; Pl. 36, fig. 8), both possibly artifacts of preservation. Morphologic variability broad, including I-, J-, C-, U-, S-shaped, and open spiral forms, with a preference for rectilinearity, particularly in short individuals. The widest forms occurring in the Rusty shale unit, a black shale in which the flattening of the cylinders has been more extensive than in the dolomitic rhythmites of the lower part of the Little Dal Group, in which occur even three-dimensionally preserved specimens.

Certain rare specimens exhibiting numerous scattered small black discs (pyritic?), uniformly about 0·2 mm across (Pl. 35, figs. 6, 7). Three-dimensionally preserved specimens associated with 'molar-tooth' structure (text-fig. 4), and showing opaque, disrupted walls, about 1 μm thick, of black kerogen with patterns of cracks due to syneresis or displacement by crystal growth (Pl. 37, fig. 5). The fossils filled with clear, pure (based on electron microprobe analysis), xenotopic, equigranular calcite (microspar?) that weathers to a medium bluish grey colour and has a grain size of about 10 μm. The matrix surrounding the fossils heterogeneous and darker, dolomitic and argillaceous, finely laminated, buff weathering, and characterized chemically by abundant K, Al, Si, Mg, and Ca.

Occurrence. Localities 1–5.

Discussion. The new material provides a basis for further insight into aspects of *Tawuia* biology, taphonomy, and nomenclature, but also leaves certain questions unresolved. First, several specimens have large numbers of submillimetric discs of uniform size (Pl. 35, figs. 6, 7). These are of considerable interest because they may provide a possible link between *Tawuia* and *Chuaria*, and relate them to the algae. Such a relationship has been inferred on the basis of the close association of isolated specimens of both taxa, and the seemingly gradational size and shape variation between the two (Hofmann 1981, p. 421; Duan 1982). If the minute discs are not diagenetic artifacts, which remains an alternative, they could be interpreted as reproductive structures. One can only speculate if, after release from *Tawuia*



TEXT-FIG. 4. Slab with three-dimensionally preserved specimens of *Tawuia dalensis*, *Chuaria circularis*, and *Tyrasotaenia*? sp., and 'molar-tooth' structure (dark linear pattern); ×0·42. Specimens of 'molar-tooth', *Chuaria*, and *Tawuia* in lower right corner of slab are shown in vertical section in Plate 37, fig. 1; specimen in upper left corner shown in Plate 36, fig. 10 and Plate 37, fig. 4.

individuals these could have grown, first isometrically to millimetric spheroids, and subsequently by allometric growth to the *Tawuia* stage, as suggested by data in text-fig. 3.

One difficulty with this hypothesis is that there are many more known occurrences of *Chuaria* than of *Tawuia* (Hofmann 1985, fig. 3). Another is the unique occurrence of a linear array of identically sized, and possibly consanguineous, overlapping discs of *Chuaria* from the 850 Ma old Uinta Mountain Group (Hofmann 1977, fig. 2a). This string of discs, if indeed consanguineous, would also disallow the idea of a postulated *Chuaria–Tawuia* relationship.

The nature and function of the disc-like terminal structure (Pl. 35, fig. 3; Pl. 36, figs. 1, 11) remain obscure. It may be a purely preservational artifact resulting from the compression of a roundly terminated cylinder with a resistant, pliable membrane, like longitudinal, oblique, and concentric wrinkles such as shown in Plate 36, fig. 1. The tapering of other specimens, particularly the more tightly bent ones (Pl. 36, fig. 3), may represent cylinders already partially deflated at the time of embedding, or abnormal specimens.

The axial to off-axial stripe of a number of specimens is more problematical. The possibility that the stripe, because of its position, might represent an alimentary canal, and the organism a metazoan, has been considered and rejected for lack of compelling evidence. The carbonaceous composition combined with the lack of any recognizable body opening, which should be of corresponding size, or other identifiable organs (e.g. structures indicating musculature or active motility), make such an interpretation difficult.

The three-dimensional preservation of *Tawuia* (and *Chuaria*) specimens indicates a heterogeneous constitution for the organisms, with a resistant test and a readily decomposed interior that is replaced by calcite. The close association of three-dimensionally preserved, calcite-filled specimens and crumpled planar features ('molar-tooth' structure) filled with identical equigranular microcrystalline calcite is noteworthy (Pl. 37, fig. 1; text-fig. 4). The black, kerogenous envelope outlining the fossils is absent in the 'molar-tooth' structure, a significant difference. Both types of structure reflect similar peculiar diagenetic conditions, and they bear on the controversial origin of 'molar-tooth' structure,

EXPLANATION OF PLATE 36

Carbonaceous compressions and three-dimensionally preserved specimens of *Tawuia dalensis* Hofmann (figs. 1–5, 7–11), *Chuaria circularis* Walcott (figs. 6, 12), and *Tyrasotaenia*? sp. (fig. 12).

Specimens in Figs. 4–7, 9, 10, 12 all on slab shown in text-fig. 4.

Fig. 1. *T. dalensis* Hofmann; clustered specimens showing various types of wrinkles. Locality 3. GSC 77192, × 4.

Fig. 2. *T. dalensis* Hofmann; specimen with granulate markings. Locality 4. GSC 77193, × 4.

Fig. 3. *T. dalensis* Hofmann; strongly tapering, curved specimen. Locality 1. GSC 77194, × 4.

Fig. 4. *T. dalensis* Hofmann; U-shaped specimen preserved three-dimensionally, showing round, uncompressed termini. Locality 1. GSC 77183, × 4.

Fig. 5. *T. dalensis* Hofmann; uncompressed, slightly tapered, with *Tyrasotaenia*? sp. at one end. Locality 1. GSC 77184, × 4.

Fig. 6. *C. circularis* Walcott; three-dimensional specimen with indentations due to burial. Locality 1. GSC 77185, × 4.

Fig. 7. *Tawuia dalensis* Hofmann; three-dimensional, C-shaped specimen with medial, longitudinal fold. Locality 1. GSC 77186, × 4.

Fig. 8. *T. dalensis* Hofmann; U-shaped compression with axial marking. Compare with fig. 7. Locality 1. GSC 77195, × 4.

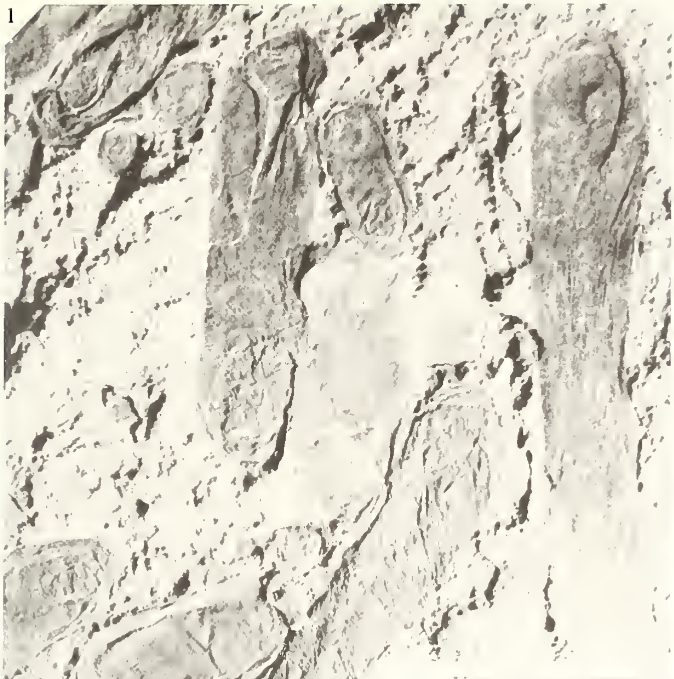
Fig. 9. *T. dalensis* Hofmann; tapering, three-dimensional specimen with collapsed central region. Compare with *Pumilibaxa huaiheiana* Zheng. Locality 1. GSC 77187, × 4.

Fig. 10. *T. dalensis* Hofmann; U-shaped specimen with oblique fold, shown in thin section view in Plate 3, figs. 4–6. Locality 1. GSC 77188, × 4.

Fig. 11. *T. dalensis* Hofmann; coiled specimen with terminal disc. Locality 1. GSC 77196, × 4.

Fig. 12. *C. circularis* Walcott overlain by thin layer of matrix with cross-sections of specimens of *Tyrasotaenia*? sp. Locality 1. GSC 77189, × 10.

PLATE 36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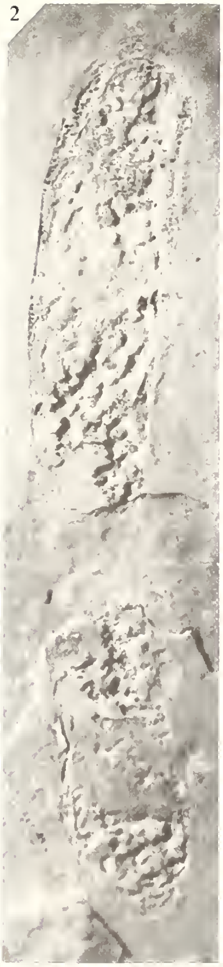
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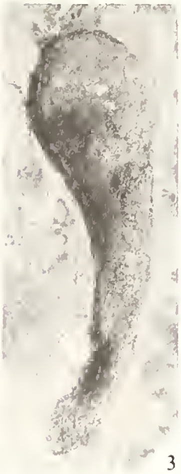
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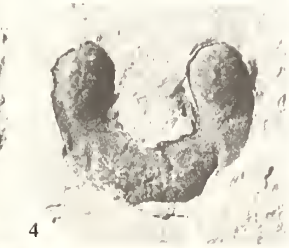
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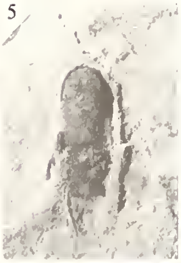
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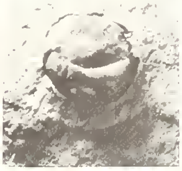
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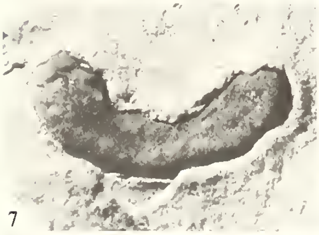
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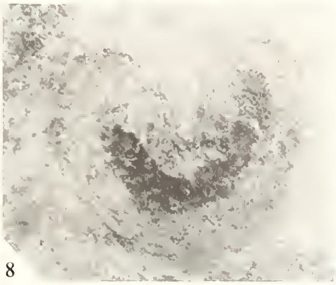
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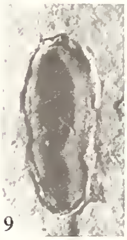
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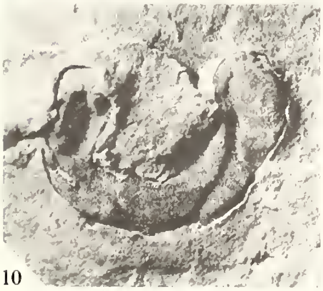
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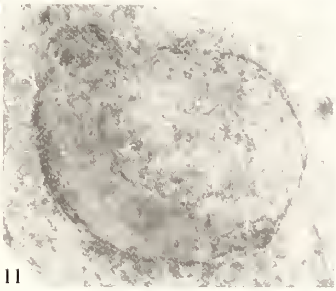
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HOFMANN, *mid-Proterozoic macrofossils*

discussed by Smith (1968) and O'Connor (1972). Both authors favoured a biogenic origin for this phenomenon, citing in evidence the occasional close association with stromatolites, and the presence of cell remains in some 'molar-tooth' sheets (O'Connor 1972, p. 606). The evidence for a biological contribution is, nevertheless, circumstantial and weak, and the purported microbes may be accidentally lodged in the cracks without playing a constructive role in its formation. The angulate patterns of the contorted thin vertical sheets indicate that a mechanical explanation (syneresis) is to be sought to explain the Little Dal 'molar-tooth' structures, such as mineral-filled cracks forming under water at the limits of influence of competing small, equally spaced tension domains, analogous to those resulting in the development of contraction cells in the formation of mudcracks or columnar basalt.

The considerable compaction indicated by the crumpled planar features (Pl 37, fig. 1), the relative lack of compaction of the fossils, and the identical nature of the equigranular microcrystalline calcite fillings, all indicate that the fillings in both are an early diagenetic phenomenon: three-dimensional shapes are chemically filled, providing some rigidity to them, before substantial compaction of the less rigid surrounding sediment occurred. The still-intact walls of the entombed organisms prevented the mechanical entry of impurities, whereas the voids created by inferred syneresis cracking provided loci for precipitation resulting in 'molar-tooth' structure. Conditions of unusual concentration of certain ions may have been a factor involved in this precipitation: elevated salinity, organic compounds, and carbonate gels come to mind. Little is known about carbonate gels, and they seem unlikely, considering the ease of crystallization of $CaCO_3$, but reference to them has been made by Lebedev (1967, pp. 24–29). As the sediment compacted (more than 50%, judging from the shortening shown in Pl. 37, fig. 1), the more rigid, vertically extensive, tabular struts of the 'molar-tooth' structure were crumpled, resulting in the disharmonic folds (reminiscent of ptygmatic folds in migmatites). By comparison the very limited vertical extent of the fossils resulted in little or no perceptible disharmonic folding during compaction, leaving the shapes much as they were at the time of burial, and probably in life. The timing of the filling by equigranular microcrystalline calcite, and the composition and physical properties of the surrounding, dewatering matrix were crucial elements whose combination resulted in such extraordinarily well-preserved Proterozoic macrofossils and this type of 'molar-tooth' structure.

EXPLANATION OF PLATE 37

All specimens are thin section views of specimens in slab illustrated in text-fig. 4. Locality 1.

Fig. 1. *Tawuia dalensis* Hofmann (upper right), *Chuaria circularis* Walcott (top middle), and 'molar-tooth' structure (left). Vertical thin section of lower right extremity of slab in text-fig. 4. The compaction of the finely laminated sediment indicated by the ptygmatoid crumpling of the 'molar-tooth' structure is at least 50%. Locality 1. GSC 77190, ×5.

Fig. 2. Enlarged view of upper left of fig. 7, showing detail of *Tawuia* wall separating fill and matrix. ×200.

Fig. 3. Enlarged view of 'molar-tooth' structure (uppermost left portion of fig. 1), showing absence of black film between calcite fill and matrix. ×50.

Fig. 4. *T. dalensis* Hofmann. Thin section of specimen in Plate 36, fig. 10, illustrating folds, preservation of carbonaceous wall, clear calcite (microspar?) fill, and heterogeneous matrix. ×5.

Fig. 5. Enlarged view of plunging fold at upper right of specimen in fig. 4, illustrating the cracked nature of the black wall material in tangential view of wall. ×125.

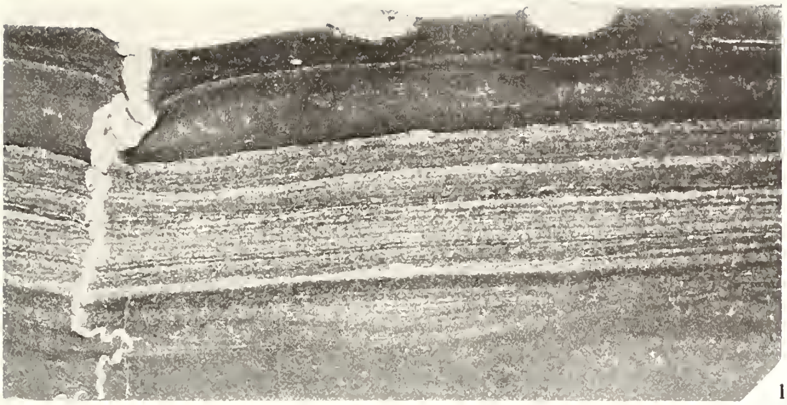
Fig. 6. Enlarged view of plunging fold near middle of specimen in fig. 4, showing nature of wall and contrast between clear calcite fill and matrix. ×25.

Fig. 7. Enlarged view of *Tawuia* specimen at upper right of fig. 1, showing folds in the wall in vertical section. GSC 77190a, ×25.

Fig. 8. *Tyrasotaenia*? sp. Enlarged view of cross-section of specimen near top middle of fig. 1, to the left and below *Chuaria* specimen. GSC 77190b, ×50.

Fig. 9. Calcite-filled voids, possibly *Tyrasotaenia*? sp. Enlarged view of portion just below *Tawuia* specimen at upper right of fig. 1. ×50.

PLATE 37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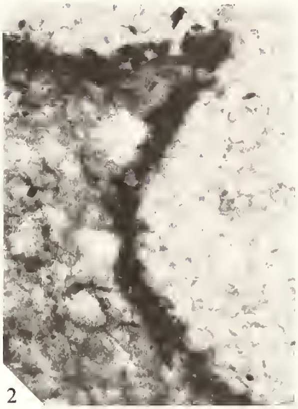
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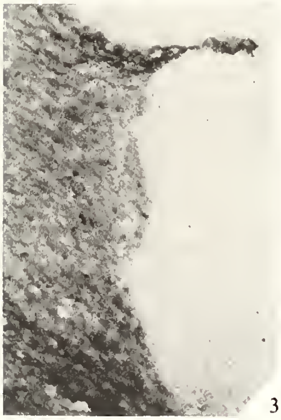
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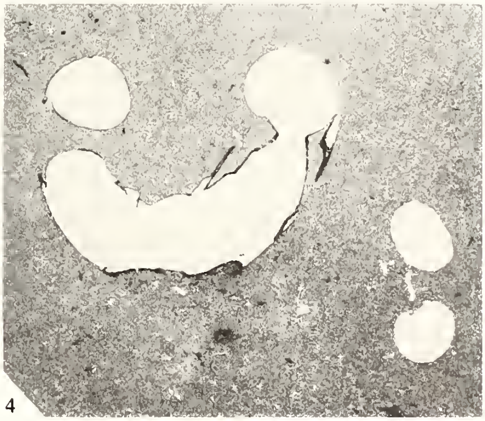
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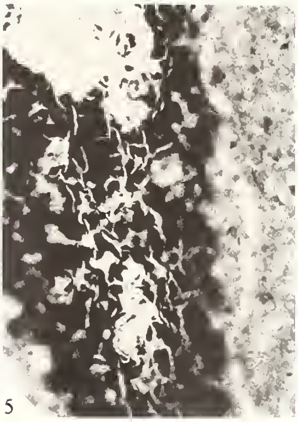
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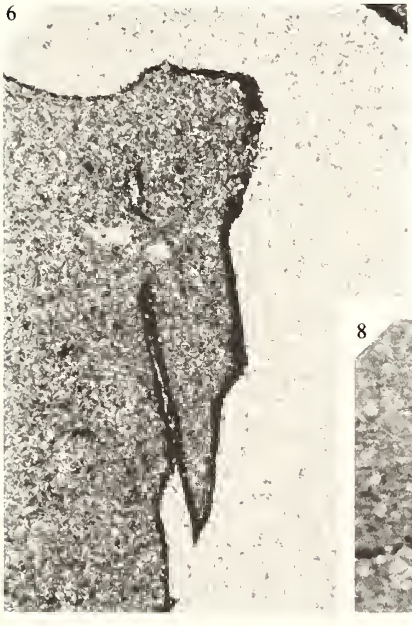

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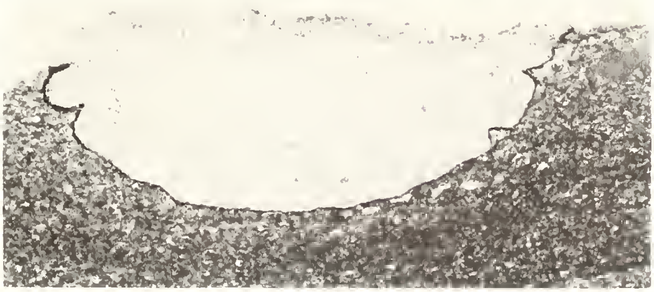

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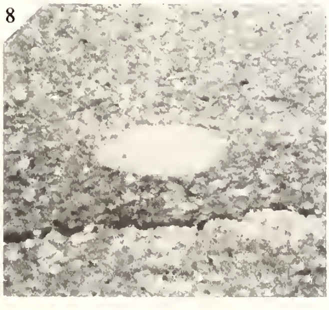

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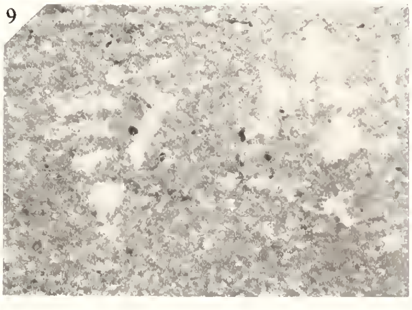


HOFMANN, *mid-Proterozoic macrofossils*

Finally, the nomenclatorial aspect of these tomaculate fossils needs to be discussed. Since the name *Tawuia* was introduced in 1979, several occurrences have been reported from other parts of the world, and a great number of new taxa have been erected (see synonymy). Three species of *Tawuia* are now named: *T. dalensis*, *T. striatia*, and *T. sinensis*. [See Note 1 added in proof, p. 353.]

T. striatia is said to be distinguished from the type species, *T. dalensis*, only by the absence of a terminal disc and by the presence of longitudinal striations. Zheng (1980) commented on the possible synonymous nature of the two species, but preferred to regard them as separate, considering the striations to be superficial features, and the terminal disc an internal structure. He did not state how many specimens were seen, and illustrated only one. Considering the wide shape (= preservational) variability among a large number of specimens of *T. dalensis*, which includes material with characteristics that could be attributed to *T. striatia*, the preferred interpretation here is to regard these two species as synonymous.

T. sinensis is reported to be somewhat narrower, shorter, and straighter than *T. dalensis* (Duan 1982), with widths averaging about 2 mm, and ranging between 1·6 and 3·5 mm, and lengths up to 29 mm. Nevertheless, the size distribution of thirty-three specimens from the Liulaobei Formation, as plotted by Duan (1982, fig. 6), is overlapped by that of *T. dalensis* from the Little Dal Group shown in text-fig. 3. Curved specimens from the same formation were assigned by Duan to *T. dalensis*. However, curvature is most likely an accidental, preservational feature rather than a biologic one, as demonstrated by specimens in the present material that includes a wide range of intermediate curvatures. *T. sinensis* can thus also be considered as probably synonymous with *T. dalensis*.

Type specimens of the other, genus-level taxa reported from Asia, and listed in the synonymy, were not seen; neither was type material of *T. dalensis* seen when those taxa were erected. Judging from the illustrations and translations of descriptions in the literature, and considering the overlapping size ranges, the great variety of preservational variants and allometric relationship of length to width exhibited by type material of *T. dalensis* from the Mackenzie Mountains, it is difficult to make distinctions between the taxa, and all those that are listed above are regarded as probable synonyms. Examples of any one of these can be seen in the present material. What is clear is that, regardless of what name has been used, the large tomaculate fossils in Asia, North America, and Europe represent a distinct group, probably of eucaryotic algae that constituted part of a widespread mid- to late Proterozoic marine macroplankton.

Before concluding this discussion, one should also mention, however, the occurrence of dark brown and black tomaculate fossils of strikingly similar size and aspect (15–25 mm by 1·8–2·5 mm), but with distinct, equally-spaced, narrow transverse markings (8–10 per mm). These are found in the Sinian System of the Shouhsien area in Anhui Province, China. They are referred to the genus *Sinosabellidites* Zheng and are assigned to the Pogonophora (Zheng 1980, p. 63). It would be interesting to determine whether the striking resemblance is merely fortuitous, or whether there could be a closer biologic affinity between *Tawuia* and *Sinosabellidites*. The latter alternative would require a rethinking of the algal interpretation for *Tawuia*, whose axial marking would assume more importance. Until more conclusive evidence for or against such a connection is developed, *Tawuia* is here regarded as distinct, and probably algal in nature.

Genus CHUARIA Walcott, 1899

Type species. Chuaria circularis Walcott, 1899.

Chuaria circularis Walcott, 1899

Plate 35, figs. 2, 4, 5, 8; Plate 36, figs. 6, 12; Plate 37, fig. 1 (partim); Plate 38, fig. 4 (partim); Plate 39, fig. 2 (partim); text-fig. 4 (partim)

Synonymy. See Duan (1982, p. 59) and Hofmann (1977, table 1).

Description. Black, carbonaceous discs with concentric wrinkles, and, less commonly, linear folds; also as impressions when film absent, and as three-dimensionally preserved oblate spheroids with accidental indentations; diameter submicroscopic to 4·5 mm; carbonaceous test of three-dimensional forms of the order of 1 μm thick extensively cracked, separating homogenous equigranular microcrystalline calcite fill from finely laminated, heterogeneous matrix.

Discussion. The mode of preservation and occurrence of *Chuaria* specimens are identical to that already discussed under *Tawuia*, and the comments made there, and the discussion about possible mutual affinities between them, need not be repeated here.

Genus LONGFENGSHANIA Du, 1982

Type species. Longfengshania stipitata Du, 1982.

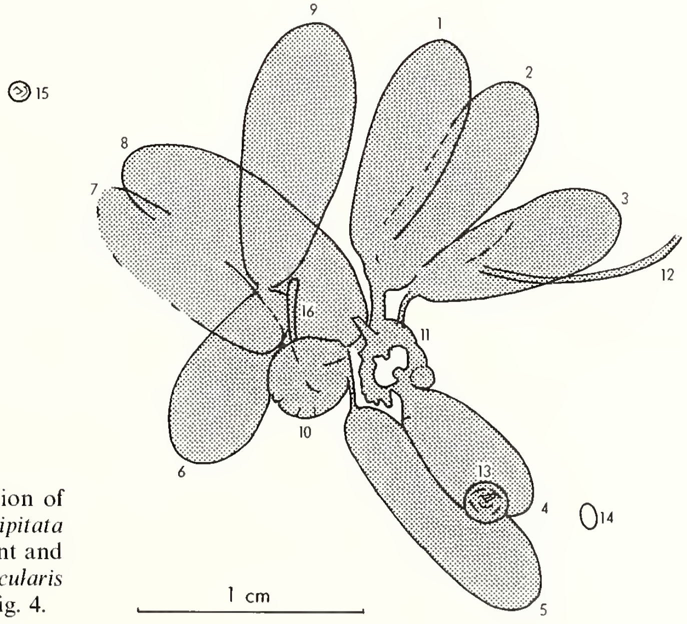
Longfengshania stipitata Du, 1982

Plate 38, fig. 4; text-fig. 5

Description. Bundles, elongate oval carbonaceous films with subradial arrangement, on bedding plane of black phosphatic and pyritic shale; compressions smooth and even, 8–12 mm long by 4 mm wide ($N = 9$); narrower, proximal end of oval film extending into a stalk-like projection or stipe, 0·5 mm or less wide and about 1 mm long. Stipes of adjoining specimens (nos. 1–4 in text-fig. 5) merging into a common, small, irregular, round carbonaceous mass several millimetres in diameter. Some ovals (nos. 1–2 in text-fig. 4) appearing to emanate from a common stipe; other individuals preserved only by partial marginal outline superimposed on more complete films (nos. 12, 16 in text-fig. 5). Specimens associated with *C. circularis* (nos. 13, 14?, 15 in text-fig. 5).

Occurrence. Locality 4.

Discussion. The structures are hardly distinguishable from those described by Du (1982) under *L. stipitata*, but they have a clustered appearance, and a subradial arrangement, with an apparent origin at a common central carbonaceous mass. The latter feature is of unusual interest, inasmuch as it suggests that the taxon represents a colony of a rather complex organism for its age, possibly an alga of phaeophyte or rhodophyte affinities, with an organ of attachment for the elongate oviform structure, somewhat like the modern *Halosaccion*.



TEXT-FIG. 5. Drawing showing interpretation of bundled specimens of *Longfengshania stipitata* Du (1–12) exhibiting subradial arrangement and superposition, and associated *Chuaria circularis* Walcott (13–15); compare with Plate 38, fig. 4.

However, before such an interpretation can be accepted, it is necessary to demonstrate beyond question that the stipe-like features are actually part of the oval compressions, and not due to fortuitous superposition of partial marginal outlines of unstiped bodies such as *Tawuia*. The latter possibility is suggested by the relationship between individuals 3 and 12 in text-fig. 4. It has not been possible to clarify this relationship for the present material, given the thinness of the films and the nature of the preservation. The type material of *L. stipitata* should be re-examined with this alternative interpretation for the stipes in mind. In fact the illustration of at least one specimen (fig. 11 of Du 1982) appears to show the stipe continuing across the oval film, curving towards the left as it crosses. Nevertheless, the close clustering of the individuals of similar size, and thus at a similar ontogenetic stage of development, and particularly their subradial orientation, with stipes towards the centre, suggest first, that a colony of stalked oviform bodies is a reasonable interpretation for now, and, secondly, that *Longfengshania* is a distinct genus.

Genus MORANIA Walcott, 1919

Type species. Morania globosa Walcott, 1919.

Morania? *antiqua* Fenton and Fenton, 1937

Synonymy. See Hofmann and Aitken (1979, pp. 160–162).

Description. Black, round carbonaceous films, with elliptical, ovate, or kidney-shaped outlines, without ornamentation, 2–11 mm across.

Discussion. Only a few specimens were seen in the present collection, so there is little new that can be added to the discussion in Hofmann and Aitken (1979). The structures may be a separate taxon, or represent compressions of globoid colonies of procaryotes.

Genus BELTINA Walcott, 1899

Type species. Beltina danai Walcott, 1899.

Beltina danai Walcott, 1899

Plate 39, figs. 5–8

Synonymy. See Hofmann and Aitken (1979, pp. 162–163).

Description. Carbonaceous films, fragmented, dark, irregular, unornamented; also smooth, brown impressions where film absent; outline irregularly angulate to smooth, oblong to equidimensional, from millimetric up to 3 × 8 cm in size; abundant on some bedding planes.

Occurrence. Localities 1 and 2.

EXPLANATION OF PLATE 38

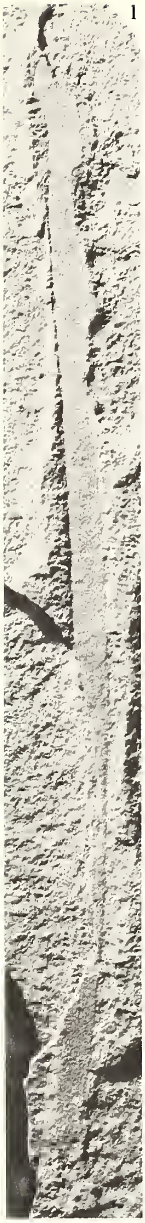
Fig. 1. Longest known specimen (an impression) of *Tawuia dalensis* Hofmann. Locality 1. GSC 77197, × 1.

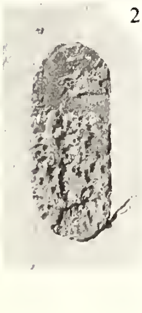
Fig. 2. *T. dalensis* Hofmann; short, pitted specimen. Locality 4. GSC 77198, × 4.

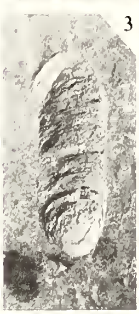
Fig. 3. *T. dalensis* Hofmann; short specimen with transverse marks. Locality 4. GSC 77199, × 4.

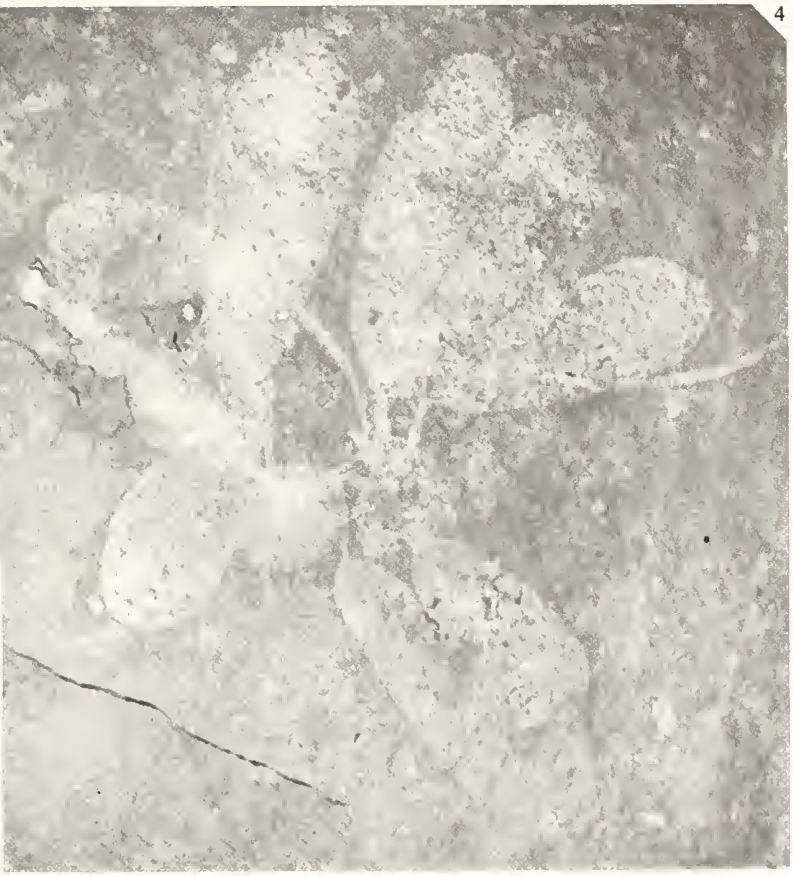
Fig. 4. *Longfengshania stipitata* Du and *Chuaria circularis* Walcott. Compare with text-fig. 5. Locality 4. GSC 77200, × 4.

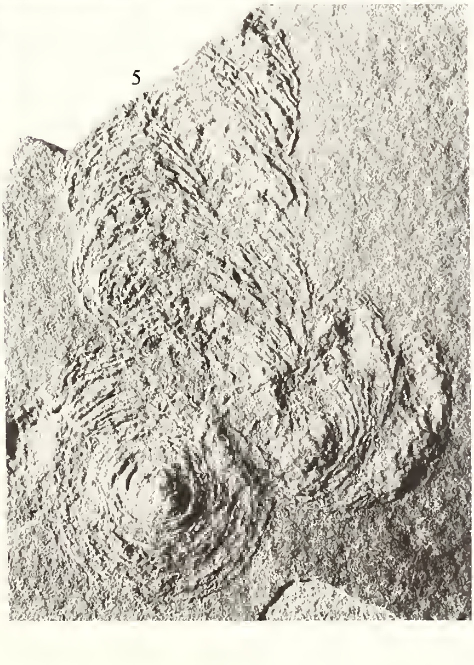
Figs. 5–6. '*Bergaueria*?' Hofmann, in Hofmann and Aitken. Structures probably inorganic, due to sapping. Locality 2. 5, GSC 77201, × 1. 6, GSC 77202, × 1.

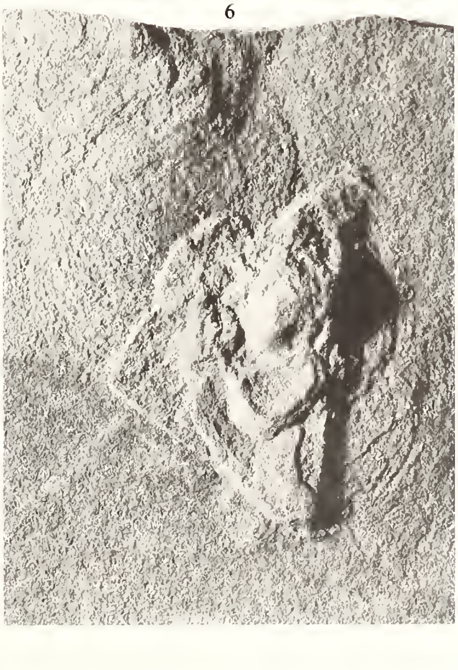












HOFMANN, *mid-Proterozoic macrofossils*

Discussion. The new material here illustrated contains fragments much larger than those previously reported from the Little Dal Group. It considerably increases the known maximum size of the parent bodies from which the fragments are derived. The taxon represents fragments of thalli, of colonies, or of organic mats. Unfortunately, the new specimens provide no further clues as to their biologic affinities.

Genus DALTAENIA gen. nov.

Type species. Daltaenia mackenziensis sp. nov.

Diagnosis. Slender, broadly curvilinear, untwisted ribbon-like structures, of uniform submillimetric to millimetric width and centimetric length; apparent infrequent lateral branching.

Etymology. Named for its occurrence in the Little Dal Group, and its ribbon-like appearance (from the Greek *taenia*, meaning ribbon).

Daltaenia mackenziensis sp. nov.

Plate 39, figs. 1–3; text-fig. 6

Diagnosis. Qualitatively, as for genus. Ribbons 0·3–1·5 mm wide.

Type specimens. Holotype: GSC 77203, specimen No. 12 in Plate 39, figs. 2, 3, and text-fig. 6; paratypes: all other numbered specimens.

Etymology. Named for its occurrence in the Mackenzie Mountains (also located in the District of Mackenzie, in the Mackenzie Mountains Supergroup).

Type locality. Section 76AC-2 in fig. 4 of Hofmann and Aitken (1979, p. 154), from interval 20 to 30 m above locality C73715.

Type lithology and horizon. Laminated, grey calcareous dolosiltite, in basinal rhythmite assemblage of Little Dal Group.

Occurrence. Locality 1.

Description. Slender, ribbon-like structures on bedding planes, partially preserved as black carbonaceus or pyritized compressions, or, where film absent, as light yellowish-grey impressions in medium grey, laminated dolosiltite; associated with abundant, similarly preserved discs of *C. circularis.* Ribbons not twisted nor tightly bent, some apparently branching (e.g. Nos. 12–13, 12–14, 12–15, 26–27 in text-fig. 6), others definitely crossing (Nos. 17–18, 29–30). Width of individuals mostly

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EXPLANATION OF PLATE 39

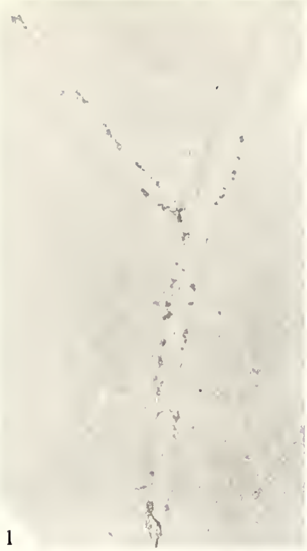
Figs. 1–3. *Daltaenia mackenziensis* gen. et sp. nov. For enumeration of specimens see text-fig. 6. Locality 1. GSC 77203. 1, upper left portion of fig. 2, showing nature of junction of specimens 29 and 30, ×4. 2, general view showing preferred orientation of specimens, and abundant small *Chuaria* in upper right of slab, ×1. 3, portion of holotype, with possible branching, ×4.

Fig. 4. *Grypania spiralis* Walter *et al.* Locality 1. GSC 77204, ×4.

Figs. 5–8. *Beltina danai* Walcott. 5, largest known specimen. Locality 1. GSC 77205, ×1. 6, second largest specimen. Locality 2. GSC 77206, ×1. 7, scattered fragments, more typical of preservation. Locality 1. GSC 77207, ×1. 8, angulate fragments. Locality 2. GSC 77208, ×1.

Figs. 9–11. *Tyrasotaenia* sp. Carbonaceous fragments of filaments. 9, Locality 2. GSC 77209, ×10. 10, long specimen. Locality 1. GSC 77210, ×10. 11, short fragment. Locality 1, GSC 77211, ×10.

PLATE 39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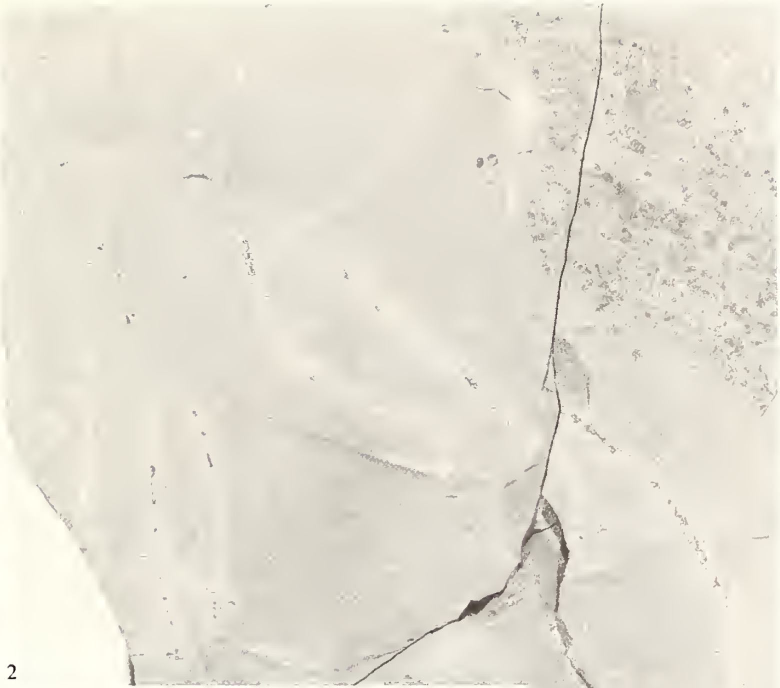
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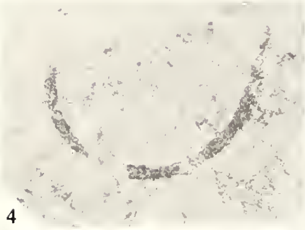
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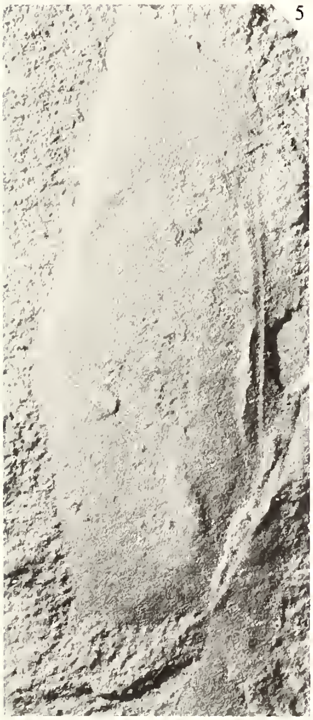
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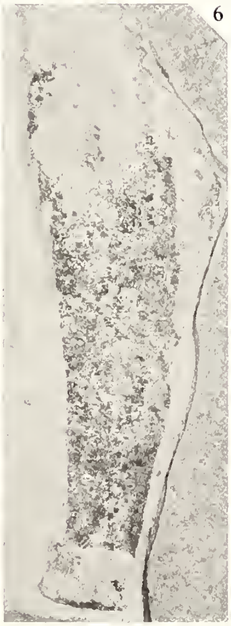
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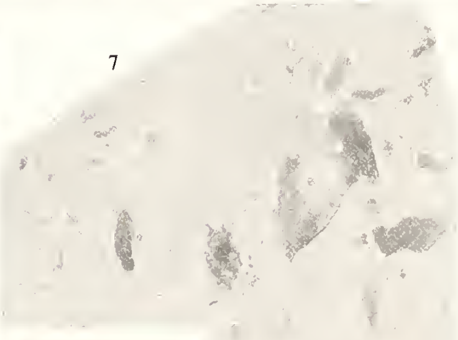
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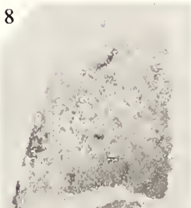
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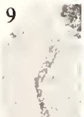
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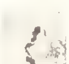
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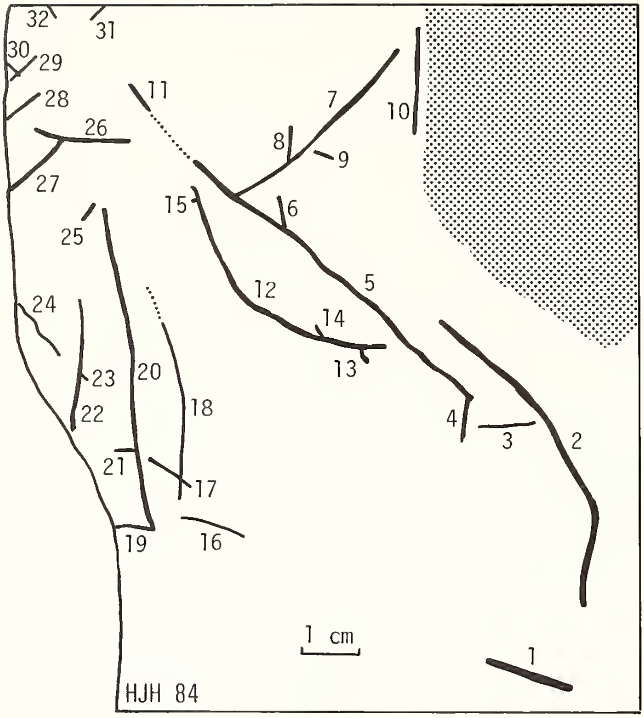
HOFMANN, *mid-Proterozoic macrofossils*



TEXT-FIG. 6. Drawing of specimens of *Daltaenia mackenziensis* gen. et sp. nov., showing numbered specimens discussed in text; compare with Plate 39, fig. 2. Stippled area contains abundant *Chuaria circularis*.

uniform, ranging from 0·3 to 1·5 mm (mean = 0·64 mm; σ = 0·29 mm; N = 32) and length of fragments from 1 to 63 mm (mean 15·8 mm). Longest structures showing some subparallel orientation, suggesting active bottom currents at time of deposition. No surface ornamentation recognized.

Discussion. The evidence for the branching nature is inconclusive. No junction definitely attributable to branching was seen. However, of the thirteen junctions preserved, as shown in text-fig. 6 (4–5, 5–6, 5–7, 7–8, 12–13, 12–14, 12–15, 17–19, 19–20, 20–21, 22–23, 26–27, and 29–30), only two (17–18 and 29–30) are clearly crossovers, leaving eleven others, some of which could be attributed to branching (12–13 looks the most convincing). These ribbons are evidently much narrower and more slender than *Tawuia*. Comparable ribbons from the Proterozoic are *Proterotainia* (Walter *et al.* 1976), represented by two species in the Helikian Belt Supergroup of Montana, and *Tyrasotaenia* (Gnilovskaya 1971) from the Vendian of eastern Europe.

Proterotainia comprises unbranched, more or less straight (may be folded), ribbon-like carbonaceous films on bedding planes, 0·1–2·0 mm in width and up to 12·5 cm or more in length; longitudinal fibrillar structure may be present. Compared to the newly reported structures, *Proterotainia* specimens show a greater degree of flexibility, including some hairpin bends.

The Vendian *Tyrasotaenia*, also unbranched, is more twisted and crumpled, and somewhat narrower, about 0·5 mm wide and up to 400 mm long. It appears to have been considerably more pliable than *Daltaenia*.

It would thus seem appropriate to recognize the distinctness of the Little Dal forms from other macroscopic ribbons previously known from the Precambrian, and to assign them to a new, genus-level taxon, *Daltaenia*, characterized by a greater rigidity, and possible branching.

Genus GRYPANIA Walter, Oehler and Oehler, 1976

Type species. Grypania spiralis (Walcott, 1899) Walter, Oehler and Oehler, 1976.

Grypania spiralis Walter, Oehler and Oehler, 1976

Plate 39, fig. 4

?1872 *Arenicolites spiralis* Billings, p. 478.
?1886 *Montfortia filiformis* Lebesconte (partim), p. 782, pl. 34, fig. 7^{II}.
?1897 *Arenicolites* (*Spiroscolex*) *spirales* Dawson, p. 53, fig. 13.
1899 *Helminthoidichnites*? *spiralis* Walcott, p. 236, pl. 26, figs. 5, 6.
?1919 Spiral impression Beer, p. 139, pl. 30. [See Note 2 added in proof, p. 353.]
?1971 *Arenicolites spiralis* Hofmann, p. 18, pl. 4, fig. 7.
1976 *Grypania spiralis* (Walcott) emend. Walter, Oehler and Oehler, n. comb., pp. 877–878, pl. 2, figs. 4–10.

Description. Single, fragmentary specimen, evenly curved, unbranched carbonaceous ribbon, 13·5 mm long, 0·5 mm wide, bent into C-shaped compression 7 mm in diameter; surface smooth to finely granulate.

Occurrence. Locality 1.

Discussion. The structure fits within *G. spiralis*, whose only previously known occurrence is in the 1·3 Ga old Greyson Shale of Montana. Other possible occurrences are cited in the synonymy, and all require re-examination. They include the structure referred to *Arenicolites spiralis* by Billings (1872) and Dawson (1897) from the late Proterozoic St. John's Group of Newfoundland (see also Hofmann 1981, pl. 18). It has thus far not been possible to relocate this specimen, nor to obtain topotypes. The identity of the Newfoundland fossil thus remains unknown. If in fact it is a *Grypania*, as is suggested by the coiled shape, the Little Dal specimen would bridge the gap between the 1·3 Ga occurrence in the Belt Supergroup and that of the approximately 0·7–0·6 Ga old St. John's Group.

Genus TYRASOTAENIA Gnilovskaya, 1971

Type species. *Tyrasotaenia podolica* Gnilovskaya, 1971.

Tyrasotaenia sp.

Plate 35, fig. 10; Plate 39, figs. 9–11

Description. Compressed fragments of slender, twisted, black carbonaceous filaments, pyritized filaments, and impressions; 80–150 μm wide, up to 7 mm long ($N = 10$); surface without ornamentation other than irregularities due to impressions of mineral grains. Specimens scattered along bedding planes, not closely crowded.

Occurrence. Localities 1 and 2.

Discussion. The carbonaceous specimens from the Mackenzie Mountains are narrower than the typical *T. podolica* from the Ukraine, but otherwise indistinguishable. They are comparable in size to specimens of *T.* sp., cf. *T. podolica* reported from the 1·8 Ga old Tuanshanzi Formation of northern China (Hofmann and Chen, 1981), and thus provide a link between much older and younger occurrences.

Tyrasotaenia? sp.

Plate 35, figs. 4 (partim), 8 (partim), 9; Plate 36, fig. 12 (partim); Plate 37, fig. 8

Description. Very slender, somewhat tortuous, three-dimensionally preserved strings, 80–150 μm wide, up to 10 mm long, preserved by bluish-grey weathering equigranular microcrystalline calcite identical to that filling specimens of *Tawuia* and *Chuaria* (see discussion under *Tawuia*); no unequivocal black carbonaceous envelope seen between fill and matrix. Some specimens bunched around three-dimensionally preserved *Chuaria* and *Tawuia*, with subradial orientation (Pl. 35, figs. 4, 8; Pl. 36, fig. 12).

Occurrence. Locality 1; seen only in beds with three-dimensionally preserved macrofossils.

Discussion. Except for their three-dimensional preservation and lack of carbonaceous envelope, these specimens differ neither in size nor shape from compressed specimens of *T.* sp. that are found on the same bedding surface. The absence of carbonaceous wall material separating fill from matrix is bothersome if one invokes the same taphonomic process as that used to explain the preservation of the larger fossils, in which carbonized cell-wall material remains; in this respect they are more like the nonbiogenic 'molar-tooth' structures. Nevertheless, one can suggest that, because the filaments are very much smaller, and thus probably also thinner walled than *Tawuia* and *Chuaria*, the absence of a carbonaceous envelope could be due to obliteration during diagenesis. The carbonaceous material is more likely to be preserved as a compression, because juxtaposition of opposite sides would double the thickness of carbonaceous material. In this interpretation *T.*? sp. and *T.* sp. would be two preservational variants of the same species.

Alternatively, the two taxa could be completely different phenomena, considering that the absence of a carbonaceous envelope is real and not due to removal after burial. A trace fossil interpretation comes to mind. In the light of present thinking among specialists as to what constitutes the oldest unquestionable evidence of burrowing activity, this occurrence would be anomalous. None the less, without dismissing this interpretation outright on theoretical grounds, several points are worth noting: First, the diameter of the structures is tiny, as might have been the inferred 1·1–0·7 Ga old originators, based on our present knowledge of metazoan evolution, and on the existence of microscopic, vasiform, heterotrophic protists in 0·9–0·7 Ga old rocks. Secondly, the structures are tortuous, like some of the earliest generally accepted trace fossils from the late Precambrian (e.g. *Torrowangea*, and some small *Planolites*), and they also have a general subradial orientation with respect to the macrofossils, as if the latter might have been points of attraction for exploitation. Mobility of such postulated primitive, microscopic heterotrophs in the substrate would have been facilitated by a high original sediment porosity before final compaction, as well demonstrated by the presence of crumpled plates of 'molar-tooth' structure. An argument against a trace fossil interpretation is the vague nature of the circumstantial evidence. The hypothesis can be tested, for instance, if they are ichnofossils, by finding the originator at one end, fecal pellets, or backfill structures; or if they are algal, by demonstrating that the termini of the strings are angulate, and the strings thus fragmental, or by finding strings with a carbonaceous envelope.

Another possibility is also briefly mentioned. The concentration of the strings around specimens of *Chuaria* could indicate that they were either part of the larger fossil, or that they represent saprophytic organisms growing on them, such as fungi. Smaller but similar such structures have been reported from the late Proterozoic of Asia under the name *Phycomycetes* (Timofeev 1969, pp. 27, 48, pl. 34, figs. 3, 5, 6) and *Mastigophycus* (Wang and Zhai 1982, p. 102, pl. 1, figs. 1–8). Alternatively, they were disparate taxa clumped mechanically during settling.

It thus seems that, although the nature of *Tyrasotaenia*? sp. is obscure, the interpretation as three-dimensionally preserved *T.* sp. seems adequate, despite the absence of a distinct carbonaceous wall.

Dubiofossil 'BERGAUERIA?' Hofmann, in Hofmann and Aitken, 1979

Plate 38, figs. 5–6

1979 *Bergaueria*? sp. Hofmann, in Hofmann and Aitken, p. 163, fig. 17C, D.

Description. Concentrically wrinkled circular to elliptical structures, 10–17 mm in diameter; isolated or juxtaposed, tapering, frond-like structures gradually widening distally; fronds composed of eccentric semicircular wrinkles of less than 1 mm relief. Preserved in medium- to fine-grained, laminated sandstone.

Occurrence. Locality 2.

Discussion. New specimens of this dubiofossil were collected in 1979 at the locality of the first find previously reported in Hofmann and Aitken (1979), and these include the counterpart to that found by

Aitken two years earlier, and illustrated in that report. Various attempts at interpreting these enigmatic structures included a trace fossil explanation (laterally moving coelenterates), and one as abiogenic markings, particularly dewatering or degassing structures. No firm conclusions were reached, and the structures were assigned to the dubiofossils.

In addition to the previously reported superficial resemblance to marks made by the modern jellyfish *Aurelia*, there is also a much more striking resemblance to a specimen illustrated as *Zoophycos* from the upper Palaeozoic of Montana (Rodriguez and Gutschick 1970, p. 433, pl. 7a). This structure, however, is distinct from other specimens in the assemblage which undoubtedly belong to this ichnogenus (R. C. Gutschick, pers. comm. 1984). Illustrations of other specimens of this '*Zoophycos*' kindly supplied by Gutschick show concentric patterns (just as the material from the Mackenzie Mountains), as well as cross-cutting relationships between different frond-like structures, making a nonbiologic origin more plausible. Possible mechanisms include gas bubbling through viscous mud slowly flowing subaerially down a gentle slope in hot spring areas. Such a mud pool interpretation has been advanced for Archean structures associated with a mineralized hydrothermal vent system in the Barberton greenstone belt (de Wit *et al.* 1982, fig. 7). A particularly striking photograph of such migrating gas escape vents in a modern setting in New Zealand is in Lloyd (1972, p. 98, fig. 63). However, the smoothly curved patterns in the illustration in de Wit *et al.* (1982) look also like some diffusion patterns produced by rhythmic precipitation (Liesegang phenomenon). The wrinkles in the structures from the Little Dal are not even or smooth, and thus unlike the diffusion banding and the mud pool structures, and they formed subaqueously in a basinal setting.

A more probable explanation is that they are sapping structures, due to dewatering. The concentric portions would represent vertically compacted dewatering channels, and the frond-like pattern would be small, vertically compacted collapse features that formed by progressive distal migration as failure occurred due to sapping in the underlying lamina during dewatering. The pattern is somewhat analogous to the crescentic slump scarps that progressively extend headward as slope failure occurs during landslide formation. Such slump scarps are also uneven, angulate crescents, as would be expected from tensional failure, and not smooth and even like pressure ridges that would result from flowage, in the opposite direction, of material being introduced into the deforming layer via the concentric structure.

The resemblance is thus closest to the questionable '*Zoophycos*' alluded to above. The fact that such similar structures occur in rocks separated in age by about half a billion years strongly supports the view that a nonbiologic mechanism is required for both; a sapping structure is thought to be a suitable explanation.

SUMMARY AND CONCLUSION

The Little Dal biota, dominated by *Tawuia* and *Chuaria*, provides an important glimpse of macroscopic life in the ocean about one billion years ago. The new collections here reported demonstrate that three-dimensional organisms could attain a size of at least 150 × 2·7 mm (after recalculating the original diameter by removing the effect of flattening). A possible biological relationship between the two taxa is suggested by their close association, by the presence of small discs attached to, or included in *Tawuia* specimens, and, possibly, by the allometric growth relationships (length/width). Evidence from other occurrences is contradictory, however, and this question remains open. The large size, the carbonaceous composition, the general shape, and the geologic age suggest that these organisms were photosynthesizing eucaryotes, probably some kind of planktonic algae.

The associated *Beltina* is also known from large fragments, at least up to 3 × 8 cm in size, further demonstrating the existence of large entities in the Proterozoic seas. But whether these are fragments of large thalli or compressions of procaryotic or eucaryotic mats or scums is still unresolved.

The specimens attributed to *Longfengshania*, with their apparent branching, are suggestive of relatively complex organisms, as is the questionably branching new genus *Daltaenia*, but conclusive branching must still be demonstrated. Their size, shape, and composition again suggest probable eucaryotic algal affinities, as do the smaller *Grypania* and *Tyrasotaenia*. The latter two represent specimens intermediate in age between previously reported occurrences, and they thus provide a link in the stratigraphic record.

Normally, the taxa are preserved as carbonaceous compressions. The extraordinary conditions leading to the three-dimensional preservation of the two dominant taxa also are responsible for the development of the 'molar-tooth' structures. Crystallization of pure equigranular microcrystalline calcite (microspar?) in both fossils and 'molar-tooth' structure was a very early diagenetic phenomenon; it occurred before compaction of the sediment, which eventually amounted to more than 50 %. The nature of these unusual conditions is not known; elevated salinity or the presence of certain organic compounds may be involved, perhaps even carbonate gels.

The three-dimensionally preserved *Tyrasotaenia*?, though occurring separately, has a slight tendency to cluster around specimens of the macrofossils, particularly *Chuaria*, suggesting a possible relationship between the two: attached filaments, saprophytic organisms, or traces of tiny organisms feeding on the larger bodies; the preferred interpretation, however, is that they are clusters of independent taxa.

Studies on the Little Dal biota are continuing, and further interesting discoveries are to be expected.

Acknowledgements. I am particularly grateful to J. D. Aitken, Geological Survey of Canada, for camp facilities, logistic support, and student assistants, for providing samples from Localities 3 and 5, and for stimulating discussions. R. Booker, S. Hermanson, and C. Viau very ably and enthusiastically assisted in the search for specimens. R. C. Gutschick provided copies of field notes and photographs of additional specimens of the '*Zoophycos*' occurrence mentioned in the paper by Rodriguez and Gutschick (1970). I thank J.-P. Bourque, M. Kachaami, P. Samson, and G. Schönbeck for technical assistance. Critical comments by J. D. Aitken, R. J. Horodyski, A. H. Knoll, and by two anonymous reviewers of earlier drafts of the typescript are gratefully acknowledged. The research was funded by the Natural Sciences and Engineering Research Council of Canada under grant No. A7484.

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NOTES ADDED IN PROOF

1. New data relevant to the discussion of *Tawuia* became available too late for inclusion in the text on p. 342. Three additional species of *Tawuia* have been proposed: *T. suketensis* (Mathur 1982, p. 128, fig. 3B; 1983*a*, p. 364, fig. 1D) and *T. rampuraensis* (Mathur 1983*a*, p. 364, fig. 1E) from the Vindhyan of India, and *T. fusiformis* (Xing 1984, pp. 34, 115, 153, pl. 21, fig. 7) from the Sinian of southern China. Specimens illustrated all resemble short specimens of *T. dalensis*. Mathur (1983*a*, p. 364, fig. 1F) also proposed a new genus and species for structures apparently identical to the *T. dalensis* illustrated in Plate 36, fig. 3.

2. The name *Spiroichnus beerii* was proposed by Mathur (1983*b*, pp. 112–113, pl. 2, figs. 1–2) for the spiral impressions reported by Beer (1919). [See synonymy for *Grypania spiralis* on p. 349.]

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OSTRACODA FROM THE MIDDLE EOCENE OF ASSAM

by JOHN W. NEALE *and* PRATAP SINGH

ABSTRACT. A traverse across the middle Eocene part of the Sylhet Formation in the Deopani Region of Assam has yielded a well-preserved Tertiary ostracod fauna. Of the twenty-nine species, twenty-two are new, one has previously been recorded elsewhere and six are left under open nomenclature. A further specimen is left under open nomenclature as a probable new subspecies of one of the new species described here. Examination of their distribution enables three successive faunas to be recognized above a lower group of beds which has not yet yielded ostracods.

The Eocene ostracod faunas of eastern India are virtually unknown and work presented here on material recovered from Assam in the Deopani traverse across the Sylhet Formation enables us to go some way towards filling this gap. The only record of ostracods from this area is by Guha (1970) who noted *Bairdia* sp., *Paracypris* sp., *Platella* sp., *Uroleberis* sp., and *Schizocythere* sp. in the middle Eocene Sylhet Limestone subcrops of Teok in a borehole drilled by the Oil and Natural Gas Commission comparable with those from Kutch in western India. In dealing with principally upper Tertiary rocks in Burma, Gramann (1975) described a small Eocene fauna of *Phalcocythere yawensis* Gramann, 1975 and *Paijenborchella* (*Eopaijenborchella*) cf. *P. eocaenica* (Triebel) and mentioned the occurrence of the genera *Cytherella*, *Cytherelloidea*, *Krithe*, and *Trachyleberis* (*Acanthocythereis*), but the nearest Burmese locality is at least 500 miles away and the fauna is of little relevance to the Assam material. There is a considerable literature on the Eocene faunas of western India and Pakistan (see Guha (1968), Khosla (1972), Khosla and Pant (1981*a*, *b*), Latham (1938), Lubimova *et al.* (1960), Siddiqui (1971, 1981) and Sohn (1970)). Guha and Shukla (1973) also described faunas of similar age from southern India but all these localities are well over a thousand miles away and, with the single exception of *Bairdia beraguaensis*, have no species in common with Assam.

Roy and Mukherjee (1976) have shown that the Mikir Hills Plataeau, an extension of the Shillong Massif, consists of an Archaean metamorphic complex and represents a foreland spur on the craton which acted as a barrier between the Himalayan Trough in the north and the Naga–Lusai Geosyncline in the south. The Massif forms a broad arch because of its greater plunge to the east and here two shelf regions of the aforementioned troughs coalesce. The Kopili Valley separates the Mikir Hills Massif from the Shillong Massif. Further west both massifs extend below the Bengal alluvium and merge with the Chotanagpur Archaean Shield.

Only the southern and south-eastern parts of the Mikir Hills Massif subsided and formed the shelf zone of the Naga–Lusai geosyncline in which middle Eocene to Quaternary sedimention took place. In consequence the southern and south-eastern parts of the Mikir Hills expose a sedimentary sequence ranging in age from middle Eocene to Pliocene and Roy and Mukherjee established the sequence in Table 1.

The present work is based on a traverse across the exposed rocks in the Dhansari Valley. Eleven samples were collected on the Deopani Traverse from 26° 13′ 11″ N, 93° 48′ 11″ E to 26° 13′ 58″ N, 93° 44′ 56″ E and all samples yielded Foraminifera except DP2. Samples DP6, DP7, DP8, DP10 have not yielded the larger Foraminifera but the smaller benthonics included *Cibicides* spp., *Heterolepa* sp., *Cycloloculina* sp., *Rotalina* sp., *Florilus* sp., *Bolivina* sp., *Discorbis* sp., *Brizalina* sp., and *Nonion* sp. Sample DP11, collected about 107 m (350 feet) above the base of the Sylhet Formation, yielded about 120 specimens belonging to eighteen species including *Linderina* sp., *Rotalia* sp., *Cibicides* sp.,

[Palaeontology, Vol. 28, Part 2, 1985, pp. 355–385, pls. 40–46.]

Heterolepa sp., *Bolivina* sp., *Discorbis* sp., *Nummulites atacicus* Leymerie, 1846, *Operculina* sp., *Anomalinella rostrata* (Brady), 1881, *Elphidium* sp., *Amphistegina* sp., *Halkyardia* sp., and miliolids. The foraminiferal assemblage is dominated by *Nummulites atacicus* and suggests a middle Eocene age.

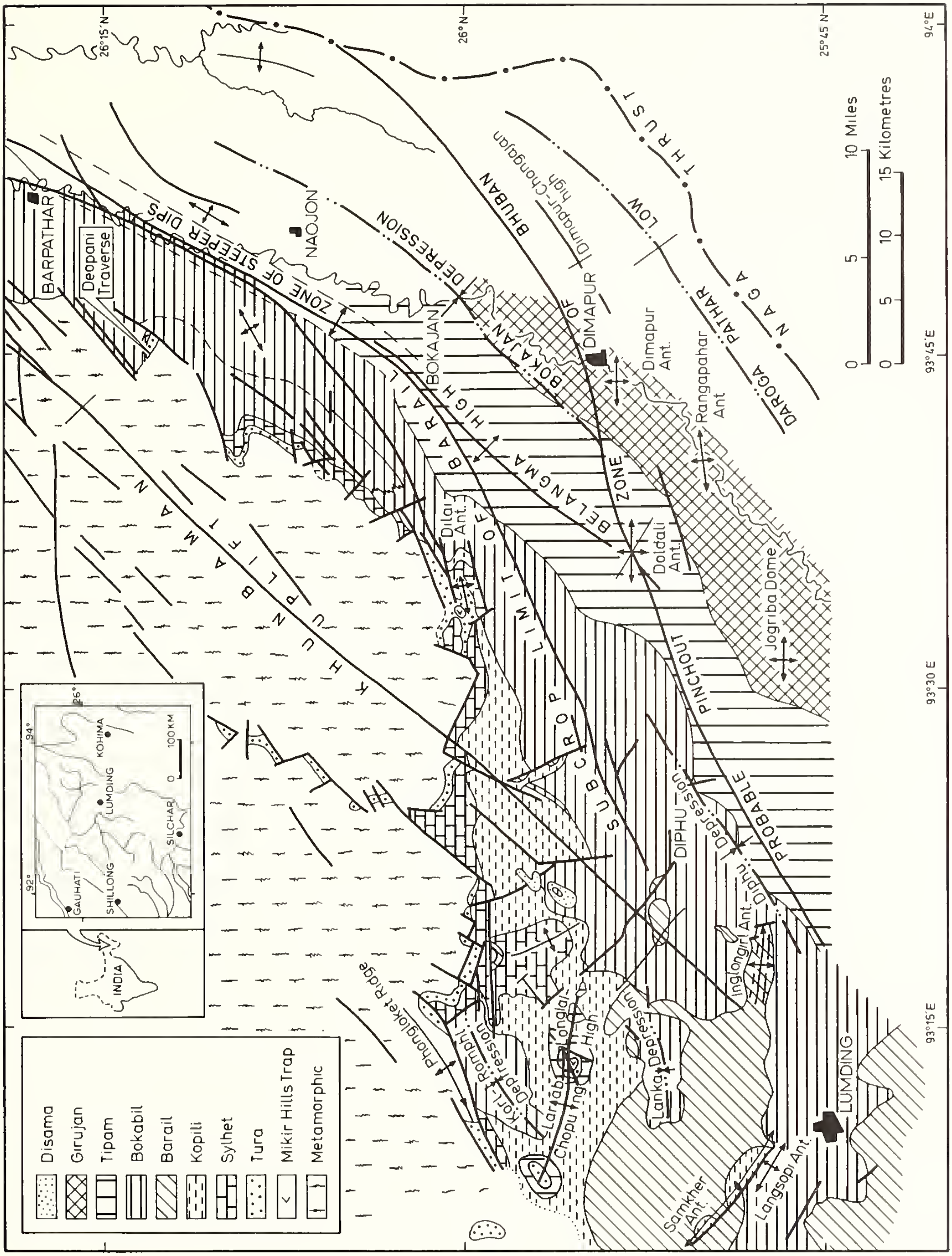
Sample DP13, a fossiliferous, light yellow, argillaceous limestone, was collected just above the contact between the Sylhet Formation and the Bokabil Formation. This contained a fairly rich assemblage of benthonic foraminiferids comprising eighty specimens of fourteen species including *Linderina* sp., *Cibicides* sp., *Planulinoides* sp., *Heterolepa* sp., *Cycloloculina* sp., *Reussella* sp., *Nummulites atacicus*, *Pararotalia* sp., *Pyrgo* sp., and miliolids which indicate a middle Eocene age. Compared with DP11 the proportion of miliolids (62·5%) is very high.

TABLE 1. General succession in the area. The Jaintia group in the subsurface of Upper Assam was divided into the Tura, Sibsagar, and Kopili Formations by Pandey (unpublished O.N.G.C. report, 1972). In the latter, Pandey proposed the term 'Sibsagar Formation' for a shale limestone unit occurring above the Tura and below the Kopili in the Upper Assam sequence, homotaxial with the 'Sylhet' of the Mikir Hills and Prang Formation (in part) of Meghalaya State, Assam. The term Sibsagar Formation was extended to include the 'Sylhet' strata of the Mikir Hills (Mohan, unpublished report 1973) in order to avoid using the term 'Sylhet' since the latter was originally proposed for a group of limestone and sandstone strata in the Khasi and Jaintia Hills of Meghalaya State which range in age from late Paleocene to middle Eocene. The 'Sylhet' of the Mikir Hills has close lithological similarities to, and is coeval with, the Sibsagar Formation but the term has been retained here following the usage of the field mapping parties.

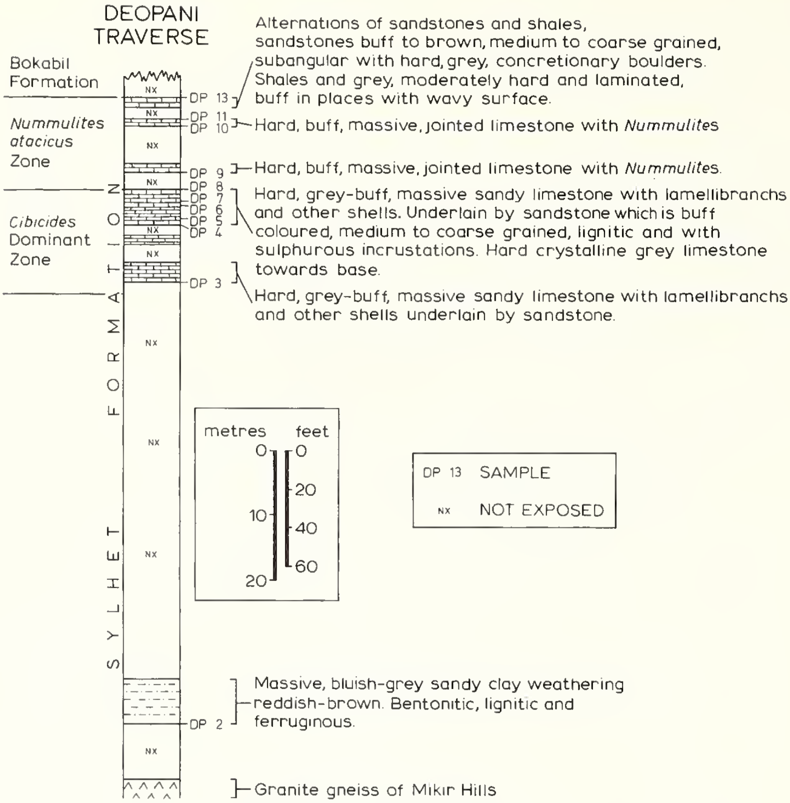
AGE	GROUP	FORMATION	APP. THICKNESS IN METRES
Quaternary		Alluvium and terrace deposits	
		-- Unconformity -----	
		Disama Formation	15+
	----------	Unconformity -----	
Neogene	Tipam	Girujan Formation	300+
		Tipam Formation	600
	Surma	Boka Bil Formation } Harihajan Mbr. Bhelijan Mbr.	900
	----------	Unconformity -----	
Paleogene	Barail	Not subdivided	400
	Jaintia	Kopili Formation	350
		Sylhet Formation	155
		Tura Formation	30
	----------	Unconformity -----	
Pre-Tertiary	Mikir Hills Trap		10
	----------	Unconformity -----	
Pre-Cambrian	Metamorphic complex		

SYSTEMATIC PALAEONTOLOGY

Diagnoses are given of new species but descriptions are superfluous since, with the exception of two single photographs on Plate 7, all specimens are figured by means of stereoscopic paired prints. Where apposite, attention is drawn to important features under 'Remarks'. All material is deposited in the Museum, Palaeontology Laboratory, Keshava Deva Malaviya Institute of Petroleum Exploration, Oil and Natural Gas Commission, Dehra Dun, whose registered numbers are given throughout.


Disama
Girujan
Tipam
Bokabil
Barail
Kopili
Sylhet
Tura
Mikir Hills Trap
Metamorphic
INDIA
GAUHATI
SHILLONG
LUMDING
KOHIMA
SILCHAR
92°
94°
26°
0
100 KM
26°15'N
26°N
25°45'N
94°E
93°45'E
93°30'E
93°15'E
0 5 10 Miles
0 5 10 15 Kilometres
BARPATHAR
Deopani Traverse
ZONE OF STEEPER DIPS
NAOJON
DEPRESSION
BHUBAN
Dimapur-Chongajan high
LOW
THRUST
NAGA
PATHAR
DAROGA
DIMAPUR
Dimapur Ant.
Rangapahar Ant
BOKAJAN
BOKAJAN
HIGH
BARAIL
BELANGMAMA
ZONE
Dilai Ant.
Doldali Ant.
OF
LIMIT
CROP
SUB
KHUNBAMAN UPLIFT
PINCHOUT
Jogriba Dome
PROBABLE
DIPHU
Depression
Diphu Ant.
Inglongiri Ant.
Diphu Depression
Phonglokot Ridge
Rompni Depression
Koti Depression
Larabi
Longlai High
Chopu
Lanka Depression
Samkher Ant.
Langsopi Ant.
LUMDING

TEXT-FIG. 1. Location of the Deopani Traverse (after Roy *et al.*, 1975).


DEOPANI TRAVERSE
Bokabil Formation
Nummulites atacicus Zone
Cibicides Dominant Zone
SYLHET FORMATION
NX
DP 13
DP 11
DP 10
DP 9
DP 8
DP 7
DP 6
DP 5
DP 4
DP 3
DP 2
Alternations of sandstones and shales, sandstones buff to brown, medium to coarse grained, subangular with hard, grey, concretionary boulders. Shales and grey, moderately hard and laminated, buff in places with wavy surface.
Hard, buff, massive, jointed limestone with Nummulites
Hard, buff, massive, jointed limestone with Nummulites.
Hard, grey-buff, massive sandy limestone with lamellibranchs and other shells. Underlain by sandstone which is buff coloured, medium to coarse grained, lignitic and with sulphurous incrustations. Hard crystalline grey limestone towards base.
Hard, grey-buff, massive sandy limestone with lamellibranchs and other shells underlain by sandstone.
metres
feet
0
10
20
0
20
40
60
DP 13 SAMPLE
NX NOT EXPOSED
Massive, bluish-grey sandy clay weathering reddish-brown. Bentonitic, lignitic and ferruginous.
Granite gneiss of Mikir Hills

TEXT-FIG. 2. Position of samples and lithology in the Deopani Traverse.

Subclass OSTRACODA Latreille, 1806
Order PODOCOPIDA Muller, 1894
Suborder PLATYCOPINA Sars, 1866
Genus CYTHERELLA Jones, 1849
Cytherella deopanica sp. nov.

Plate 40, figs. 1–5

Holotype. A male carapace, IPE/H02/03/979.

Paratypes. One male and three female carapaces and valve IPE/P02/03/978, 1032, 1033, 1037.

Type horizon. DP6.

Derivation of name. After the location of the traverse along the Deopani River.

Dimensions of figured specimens.

	Length	Height	Width
Holotype, male carapace, IPE/H02/03/979	668 μm	348 μm	312 μm
Paratype, male carapace, IPE/P02/03/978	652 μm	354 μm	280 μm
Paratype, female right valve, IPE/P02/03/1037	670 μm	410 μm	190 μm
Paratype, female carapace, IPE/P02/03/1033	650 μm	440 μm	345 μm
Paratype, female carapace, IPE/P02/03/1032	660 μm	440 μm	390 μm

Diagnosis. A *Cytherella* which in side view is narrower anteriorly than posteriorly, with a distinct dorsal angle at, or immediately behind mid-height. Anterior dorsal margin straight, posterior margin rounded with the right valve overlapping the left valve all the way round. Surface faintly pitted. Greatest width at two-thirds (male) or three-quarters (female) length.

Remarks. C. deopanica is perhaps closest to *C. sylvesterbradleyi* Reyment, 1963 from the late Paleocene of Nigeria as figured by Foster *et al.* (1983) where there is close correspondence in dorsal view. The overlap of the left valve by the right in side view is more uniform, however, and is particularly well seen in the posterior region; the anterodorsal margin is straighter. These comments are less applicable to the holotype figured by Reyment (1963, pl. 1, fig. 1) but in that specimen the height is much greater in proportion to the length, the greatest height lies much further posteriorly and the outline tapers less anteriorly. *C. utilis* Bertels, 1968 from the Maastrichtian and *C.* sp. aff. *C. utilis* Bertels, 1973 from the lower Tertiary of Argentina have the greatest height more posteriorly in lateral view and the anterodorsal margin is distinctly concave. *C. unguiformis* Kollmann, 1962 from the middle Eocene of Istria (Jugoslavia) is generally similar but differs in the more concave anterodorsal margin, the lesser taper anteriorly and the lack of overlap of the left valve by the right valve posteroventrally in side view. *C. montensis* Marlière, 1958 from the Montian of Belgium is shorter in proportion to the length and lacks the pitted surface.

Cytherella assamensis sp. nov.

Plate 40, figs. 6–9

Holotype. ?Male carapace IPE/H02/03/1036.

Paratype. Three ?female carapaces and valves IPE/P02/03/1034, 1035, 1038.

Type horizon. DP8.

Derivation of name. From the State of Assam.

Dimensions of figured specimens.

	Length	Height	Width
Paratype, ?female carapace, IPE/P02/03/1034	465 μm	310 μm	215 μm
Paratype, ?female carapace, IPE/P02/03/1035	430 μm	295 μm	210 μm
Holotype, ?male carapace, IPE/H02/03/1036	540 μm	350 μm	245 μm
Paratype, ?female carapace, IPE/P02/03/1038	650 μm	440 μm	215 μm

Diagnosis. In lateral view oval, tapering strongly posteriorly where it is much more narrowly rounded than anteriorly. Greatest height immediately behind mid-length, pitted surface. The shell is characteristically 'pinched in' just below the anterodorsal margin so that the latter gives the impression of a slight ridge. Overlap of the left valve by the right valve is complete but slight. Sexes difficult to differentiate.

Remarks. Whilst comparable in no other way the specimen of *C. sylvesterbradleyi* Reyment figured by Foster *et al.* (1983, pl. 14, fig. 6) from the late Paleocene of Nigeria shows a similar 'pinching in' of the anterodorsal margin and pitting. Compared with *Platella guzeratensis* of Guha (1965) from the Paleogene of Gujarat State the present species tapers more posteriorly and lacks the prominent subcentral depression. *C. rajui* Guha and Shukla, 1973 from the lower Eocene of Virdhachalam, Tamilnadu (11° 39′ 45″ N, 79° 23′ 47″ E; 11° 37′ N, 79° 18′ 12″ E) is difficult to interpret because if their pl. 1, fig. 19 is a right valve as stated, it appears that their pl. 1, fig. 4 must be a left valve and not a right valve. If this interpretation is correct the shape is somewhat similar but it lacks the pinching in below the anterodorsal margin and the surface is smooth.

Cytherella barpatharensis sp. nov.

Plate 40, figs. 10–12

Holotype. Male carapace IPE/H02/03/1043.

Paratype. Male carapace IPE/P02/03/1060, female carapace IPE/P02/03/1049.

Type horizon. DP8.

Derivation of name. From the town of Barpathar which lies north-east of the Deopani Traverse.

Dimensions of figured specimens.

	Length	Height	Width
Paratype, male carapace, IPE/P02/03/1060	485 μm	285 μm	205 μm
Holotype, male carapace, IPE/H02/03/1034	505 μm	260 μm	170 μm
Paratype, female carapace, IPE/P02/03/1049	530 μm	300 μm	215 μm

Diagnosis. A very elongate species with the greatest height in side view at approximately two-thirds the length. Female much more vaulted posteriorly in lateral view than the male which tapers noticeably. Very compressed in dorsal view with a tendency to form a marginal rim posteriorly. Pitting fine but particularly noticeable posteriorly. Right valve overlaps the left valve all round.

Remarks. Nothing closely resembling this is reported in the literature. There is some resemblance in outline to *C. elongata* Swanson, 1969 from the upper Oligocene of New Zealand but *C. barpatharensis* differs in having a finely pitted surface and gently rounded ends.

Cytherella hastata sp. nov.

Plate 41, figs. 1–5

Holotype. Male carapace IPE/H02/03/1041.

Paratypes. Male and female carapaces IPE/P02/03/1063, 1048.

Type horizon. DP11.

Other horizons. DP13 including figured specimens IPE/B02/03/1055, 1062.

Derivation of name. Latin *Hasta* 'a spear' in reference to its shape in dorsal view.

Dimensions of figured specimens.

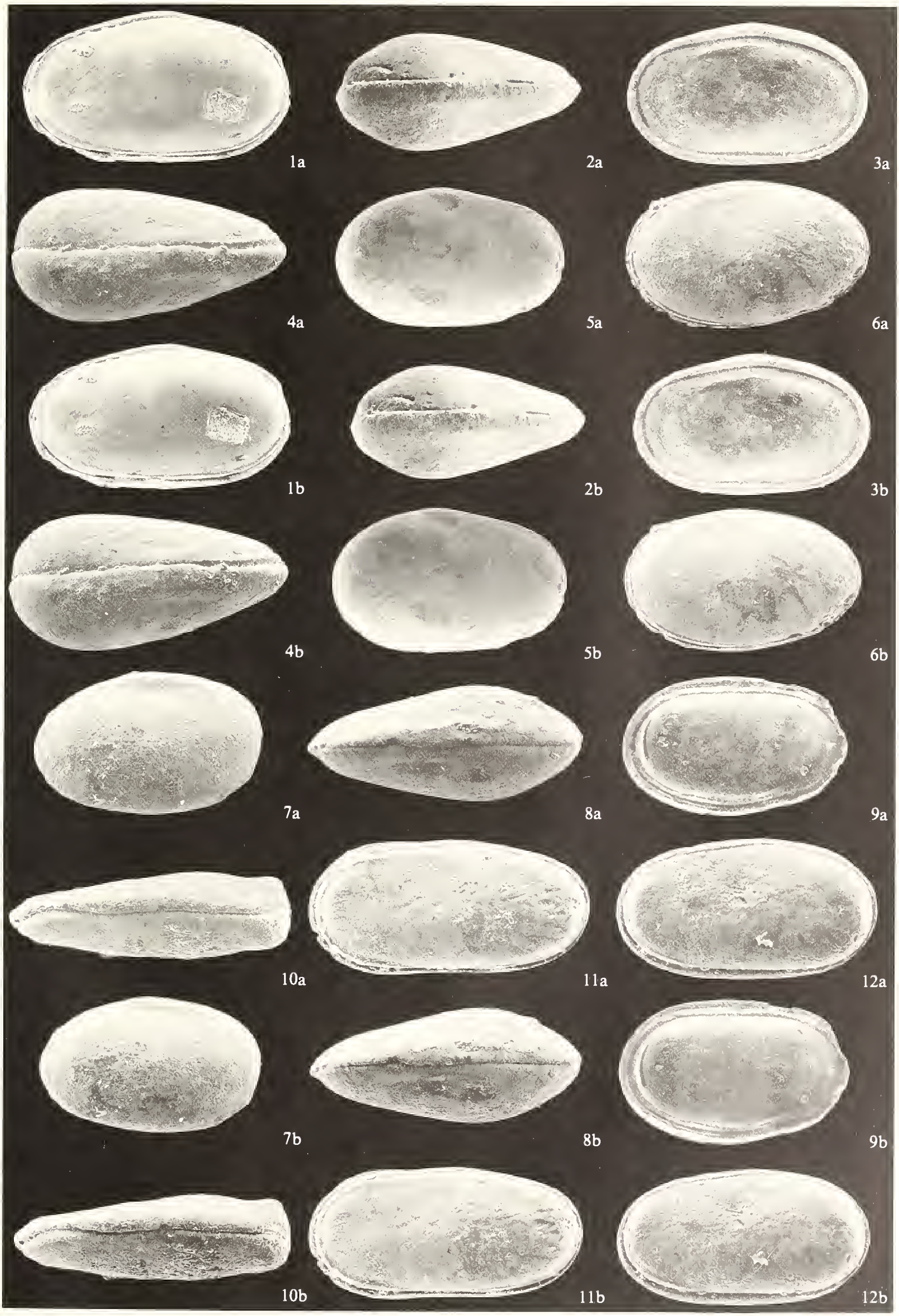
	Length	Height	Width
Holotype, male carapace, IPE/H02/03/1041	470 μm	250 μm	180 μm
Paratype, male carapace, IPE/P02/03/1063	465 μm	270 μm	190 μm
Paratype, female carapace, IPE/P02/03/1048	445 μm	255 μm	170 μm
Male carapace, IPE/B02/03/1055	440 μm	240 μm	
Female carapace, IPE/B02/03/1062	490 μm	290 μm	205 μm

EXPLANATION OF PLATE 40

Figs. 1–5. *Cytherella deopanica* sp. nov. 1, male carapace from left, holotype, IPE/H02/03/979, DP6, × 66. 2, male carapace in dorsal view, paratype, IPE/P02/03/978, DP6, × 61. 3, female right valve, internal view, paratype, IPE/P02/03/1037, DP8, × 60. 4, female carapace in dorsal view, paratype, IPE/P02/03/1033, DP8, × 70. 5, female carapace from right, paratype, IPE/P02/03/1032, DP8, × 58.

Figs. 6–9. *Cytherella assamensis* sp. nov. All from sample DP8. 6, ?female carapace from left, paratype, IPE/P02/03/1034, × 84. 7, ?female carapace from right, paratype, IPE/P02/03/1035, × 88. 8, ?male carapace in dorsal view, holotype, IPE/H02/03/1036, × 76. 9, ?female right valve, internal view, paratype, IPE/P02/03/1038, × 57.

Figs. 10–12. *Cytherella barpatharensis* sp. nov.. All from sample DP8. 10, male carapace in dorsal view, paratype, IPE/P02/03/1060, × 94. 11, male carapace from left, holotype, IPE/H02/03/1043, × 91. 12, female carapace from left, paratype, IPE/P02/03/1049, × 81.


1a
2a
3a
4a
5a
6a
1b
2b
3b
4b
5b
6b
7a
8a
9a
10a
11a
12a
7b
8b
9b
10b
11b
12b

NEALE and SINGH, *Cytherella*

Diagnosis. Carapace elongate and pitted, tapering posteriorly with the greatest width at approximately three-quarters length in the male and a little more posteriorly in the female. Greatest height behind the mid-length in the male (Pl. 41, fig. 2) and at about two-thirds length in the female (Pl. 41, fig. 3). The carapace anterior of the greatest height is almost parallel sided, tapering only slightly, whereas posteriorly it tapers strongly. The pitting is strongest in the posterior third of the shell but varies greatly according to preservation (cf. Pl. 2, figs. 1, 4).

Remarks. The more strongly pitted forms came from DP13 but there seems no good reason to regard them as specifically distinct. There is some resemblance to *C. terminopunctata* Holden, 1964 as figured by Bertels (1975) from the middle Maastrichtian of Argentina but the posterior punctation is more marked in the Indian species and the shape of the male in the Argentine species corresponds more closely in shape with the female of *C. hastata* and is very different from the male of the Indian species. There are no other closely comparable forms figured in the literature.

Cytherella antheriformis sp. nov.

Plate 41, figs. 6–9

Holotype. Male carapace IPE/H02/03/941.

Type horizon. DP8.

Derivation of name. From its resemblance to the anther of a flowering plant when seen in dorsal view.

Dimensions of figured specimen.

	Length	Height	Width
Holotype, male carapace, IPE/H02/03/941	440 μm	235 μm	200μm
Other figured specimens lost.			

Diagnosis. The coarsely pitted carapace tapers anteriorly with the greatest height at approximately three-quarters length. Anterodorsal margin long and straight, sloping gently anteriorly, posterodorsal margin merging into the evenly rounded posterior margin. Ventral margin gently convex. Sexual dimorphism very marked with the males much longer in proportion to the height than the females. In dorsal view the greatest width is at about three quarters length, the females being much wider than the males.

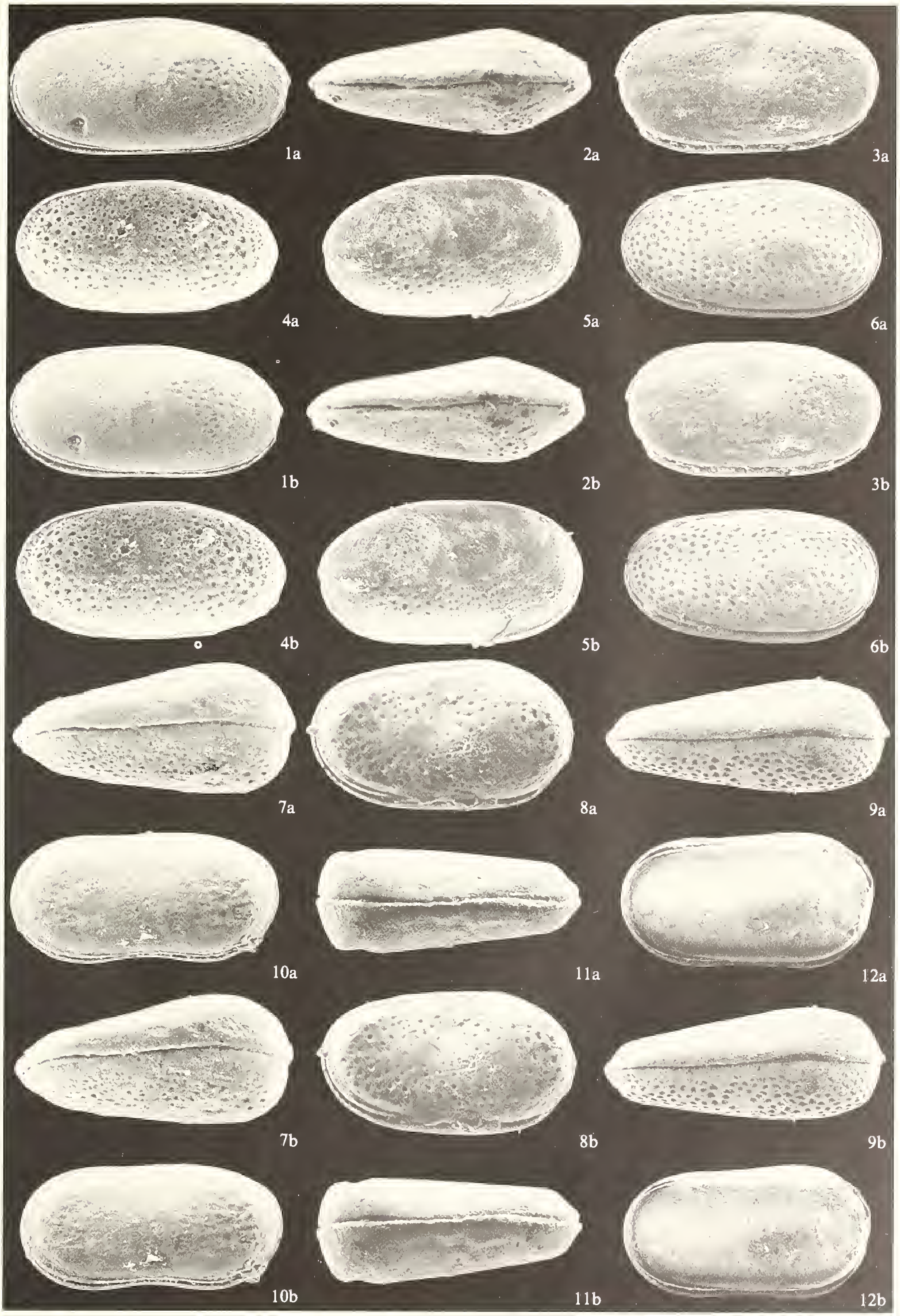
Remarks. This differs from the previous species in the anterior tapering of the carapace seen in side view and the stronger punctation. There are no closely comparable species figured in the literature.

EXPLANATION OF PLATE 41

Figs. 1–5. *Cytherella hastata* sp. nov. 1–3 from sample DP11; 4, 5 from sample DP13. 1, male carapace from left, holotype, IPE/H02/03/1041, × 98. 2, male carapace in dorsal view, paratype, IPE/P02/03/1063, × 99. 3, female carapace from left, paratype, IPE/P02/03/1048, × 97. 4, male carapace from left, IPE/B02/03/1055, × 98. 5, female carapace from right, IPE/B02/03/1062, × 86.

Figs. 6–9. *Cytherella antheriformis* sp. nov. 6, male carapace from left, holotype, IPE/H02/03/941, DP11, × 95. 7, female carapace in dorsal view, specimen lost, DP8. 8, female carapace from left, specimen lost, DP8. 9, male carapace in dorsal view, specimen lost, DP8.

Figs. 10–12. *Cytherella ventroconcava* sp. nov. All from sample DP11. 10, male carapace from left, holotype, IPE/H02/03/1042, × 105. 11, male carapace in dorsal view, paratype, IPE/P02/03/940, × 99. 12, female carapace from left, paratype, IPE/P02/03/938, × 92.


1a
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10a
11a
12a
7b
8b
9b
10b
11b
12b

NEALE and SINGH, *Cytherella*

Cytherella ventroconcava sp. nov.

Plate 41, figs. 10–12.

?1976 *Cytherella* sp. 9. Ducasse and Grekoff, pp. 138–9, pl. 1, figs. 1–2.

Holotype. Male carapace IPE/H02/03/1042.

Paratypes. Male and female carapaces IPE/P02/03/940, 938.

Horizon. DP11.

Derivation of name. From its markedly concave ventral margin in side view.

Dimensions of figured specimens.

	Length	Height	Width
Holotype, male carapace, IPE/H02/03/1042	420 μm	210 μm	150 μm
Paratype, male carapace, IPE/P02/03/940	435 μm	240 μm	200 μm
Paratype, female carapace, IPE/P02/03/938	450 μm	250 μm	200 μm

Diagnosis. In lateral view elongate with markedly concave ventral margin especially in the right valve. Anterior end evenly rounded, posterior end with supracurvature well shown in Pl. 2, fig. 10. Sexual dimorphism well developed with the female higher in proportion to the length than the male and with the greatest height at about five-sixths length. Better preserved forms show evidence of surface punctation. In dorsal view characteristically straight sided.

Remarks. The concave ventral margin and straight sides in dorsal view make this species very distinctive. It is closest to *Cytherella* sp. 9. Ducasse and Grekoff, 1976, a form recovered from the lower Eocene of DSDP Site 246 in the south-eastern Indian Ocean. Their figured specimen in lateral view shows infracurvature anteriorly and is not evenly rounded like *C. ventroconcava* but the two species are very similar in dorsal view. It is not possible to say whether Ducasse and Grekoff's (1976) specimen falls within the range of variation of the present species and so it is only tentatively referred here in the synonymy. *C. tawaica* (later corrected to *C. tawica*) Singh and Tewari, 1966 (in Tewari and Singh) from the Kalakot Formation (late early Eocene) of the Subathu Group of Jammu and Kashmir State is longer, not so markedly concave ventrally and the carapace is more pointed anteriorly in dorsal view.

Cytherella sp.

Plate 42, figs. 1, 2

Horizon. DP13.

Dimensions of figured specimens.

	Length	Height	Width
Carapace IPE/X02/03/1052	450 μm	310 μm	240 μm
Carapace IPE/X02/03/1053	430 μm	280 μm	220 μm

Remarks. It has not been possible to refer these specimens to any described species and the material is insufficient and not distinctive enough to warrant a name.

Genus CYTHERELLOIDEA Alexander, 1929

Cytherelloidea sp. juv.

Plate 42, fig. 3

Type horizon. DP8.

Dimensions of figured specimen.

	Length	Height	Width
Carapace IPE/X02/03/964	360 μm	205 μm	125 μm

Remarks. Only a single specimen of this species has been found and because of this and its small size, which suggests a juvenile, it is left under open nomenclature. It differs from *C. barkhaensis* Tewari and Tandon, 1960 from the lower Miocene of Kutch in lacking an oblique ridge extending from the posterior region to the anterodorsal region.

Suborder PODOCOPINA Sars, 1866
Superfamily BAIRDIACEA Sars, 1866
Family BAIRDIIDAE Sars, 1888
Genus BAIRDIA M'Coy, 1844
Bairdia beraguaensis Singh and Tewari, 1966

Plate 42, fig. 4

1966 *Bairdia beraguaensis* Singh and Tewari, in Tewari and Singh, pp. 119–120, pl. 1, fig. 4a–d.
1970 *Bairdia beraguaensis* Singh and Tewari; Sohn, p. 60, pl. 1, fig. 56.
1972 *Bairdia beraguaensis* Singh and Tewari; Khosla, p. 483, pl. 1, fig. 8.
1984 *Bairdia beraguaensis* Singh and Tewari; Singh, pp. 141–144.

Dimensions of figured specimen.

	Length	Height	Width
Carapace IPE/B02/03/910	940 μm	550 μm	390 μm

Remarks. This is the only species from Assam which is known from elsewhere on the Indian subcontinent. It has been described by Tewari and Singh (1966) from argillaceous limestones of late early Eocene age in Jammu and Kashmir State. The type material has been refigured by Singh (1984).

Superfamily CYPRIDACEA Baird, 1845
Family PONTOCYPRIDIDAE Muller, 1894
Genus PROPONTOCYPRIS Sylvester-Bradley, 1947
Propontocypris eocaenica sp. nov.

Plate 42, figs. 5–7

Holotype. A carapace IPE/H02/03/929.

Paratypes. Six specimens IPE/P02/03/1010, 1012, 1431–1434.

Type horizon. DP11.

Derivation of name. From its stratigraphical occurrence in the Eocene.

Dimensions of figured specimens.

	Length	Height	Width
Holotype, carapace, IPE/H02/03/929	410 μm	220 μm	165 μm
Paratype, carapace, IPE/P02/03/1012	405 μm	205 μm	160 μm
Paratype, carapace, IPE/P02/03/1010	410 μm	205 μm	165 μm

Diagnosis. A *Propontocypris* with triangular outline in side view showing anterior infracurvature, greatest height just behind one-third length and strongly tapering, narrowly rounded, posterior end.

Remarks. Fossil Cypridacea are only very rarely recorded from the Eocene of this mid-Tethyan area when they are generally referable to *Paracypris.* There is nothing closely comparable to the present form.

Family SCHIZOCYTHERIDAE Howe, 1961
Genus PAIJENBORCHELLA Kingma, 1948
Subgenus EOPAIJENBORCHELLA Keij, 1966
Paijenborchella (*Eopaijenborchella*) *assamensis* sp. nov.

Plate 42, figs. 8–12; Plate 43, figs. 1–3

Material. 142 specimens from sample DP8 and nineteen specimens from sample DP11.

Holotype. A male carapace IPE/H02/03/907.

Paratypes. Three male and four female carapaces IPE/P02/03/908, 950, 953, 997.

Type horizon. DP8.

Derivation of name. From its occurrence in Assam.

Dimensions of figured specimens.

	Length	Height	Width
Holotype, male carapace, IPE/H02/03/907	415 μm	205 μm	220 μm
Paratype, male carapace, IPE/P02/03/951	510 μm	260 μm	240 μm
Paratype, female carapace, IPE/P02/03/908	360 μm	210 μm	175 μm
Paratype, female carapace, IPE/P02/03/950	350 μm	200 μm	200 μm
Paratype, female carapace, IPE/P02/03/953	360 μm	200 μm	180 μm
Paratype, female carapace, IPE/P02/03/997	340 μm	195 μm	165 μm
Paratype, male carapace, IPE/P02/03/998	310 μm	150 μm	140 μm
Paratype, male carapace, IPE/P02/03/999	400 μm	190 μm	190 μm

Diagnosis. A species with deep median sulcus, strong mid-rib and gently convex ventral margin in side view. Strong sexual dimorphism, the females shorter in proportion to the height and wider than the males.

Remarks. Ornamentation is somewhat variable as can be seen by comparing Plate 42, figs 10 and 12 and is probably a preservational phenomenon. *P. assamensis* differs considerably from all other described species of the genus. *P. eocaenica* Triebel 1949 differs markedly in shape having a much more convex ventral outline and the same is true for *P. lomata* and *P. marssoni* Triebel, 1949. *P. tricostata* (Lienenklaus, 1900) as figured by Szczechura (1977) from the Eocene of Eastern Poland has a much more strongly developed ventral rib which gives the carapace an alate appearance and a more concave posteroventral outline amongst other differences. *P. berggreni* Krstic, 1979 from the Miocene of Iran differs in outline and the ventral rib rises strongly anteriorly; the species from the Neogene of Japan assigned to this genus by Ishizaki (1966) are much more quadrate and other recorded species are not closely comparable.

Paijenborchella (*Eopaijenborchella*) sp.

Plate 43, fig. 4

The same sample that provided the abundant specimens of *P. assamensis* also yielded a single specimen of the genus which showed strong reticulation and a short straight mid-rib. In addition the flanks of the dorsal sulcus show rows of fine pits on each flank. This appears to lie outside the range of variation shown by the previous species but because of its rarity it is here left under open nomenclature.

EXPLANATION OF PLATE 42

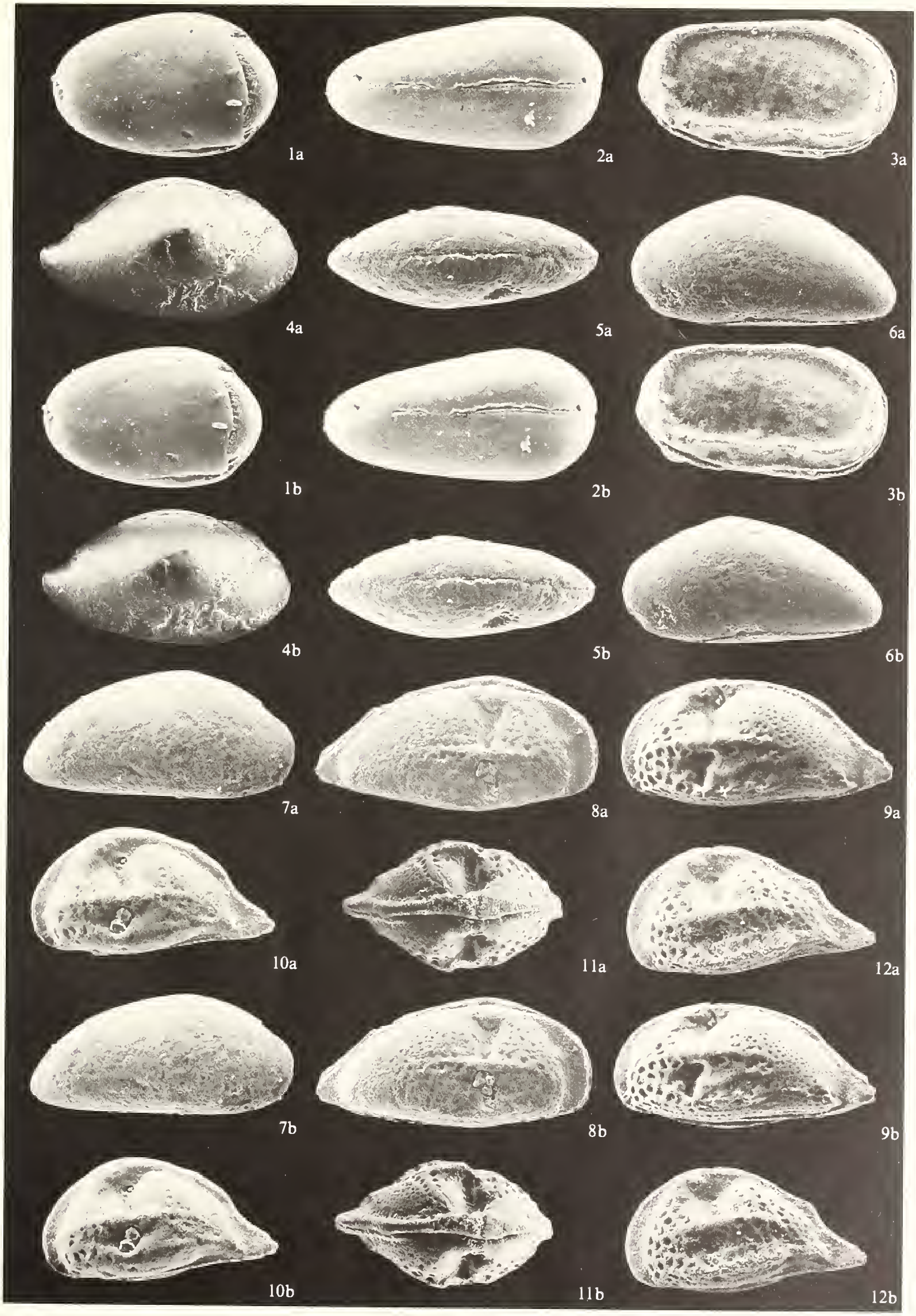
Figs. 1, 2. *Cytherella* sp. 1, carapace from left, IPE/X02/03/1052, DP13, ×82. 2, carapace in dorsal view, IPE/X02/03/1053, DP13, ×107.

Fig. 3. *Cytherelloidea* sp. juv., carapace from right, IPE/X02/03/964, DP8, ×116.

Fig. 4. *Bairdia beraguaensis* Singh and Tewari 1966, carapace from right, IPE/B02/03/910, DP13, ×45.

Figs. 5–7. *Propontocypris eocaenica* sp. nov. All from sample DP11. 5, carapace in dorsal view, paratype, IPE/P02/03/1012, ×106. 6, carapace from left, holotype, IPE/H02/03/929, ×102. 7, carapace from right, paratype, IPE/P02/03/1010, ×107.

Figs. 8–12. *Paijenborchella* (*Eopaijenborchella*) *assamensis* sp. nov. All from sample DP8. 8, male carapace from right, paratype, IPE/P02/03/951, ×90. 9, male carapace from left, holotype, IPE/H02/03/907, ×102. 10, female carapace from left, paratype, IPE/P02/03/908, ×119. 11, female carapace in dorsal view, paratype, IPE/P02/03/950, ×101. 12, female carapace from left, paratype, IPE/P02/03/953, ×114.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NEALE and SINGH, *Eocene Ostracoda*

Dimensions of figured specimen.

	Length	Height	Width
Female carapace IPE/X02/03/954	370 μm	230 μm	250 μm

Horizon. DP8.

Paijenborchella? enigma sp. nov.

Plate 43, fig. 5

Holotype. Carapace IPE/H02/03/971.

Paratype. Carapace IPE/P02/03/972.

Type horizon. DP6.

Derivation of name. From the problematic generic placing of this species.

Dimensions of figured specimen.

	Length	Height	Width
Holotype, carapace, IPE/H02/03/971	510 μm	230 μm	220 μm

Diagnosis. An elongate species with typical sulcus crossed by the median rib as in *Paijenborchella*, but lacking the characteristic drawn out posteroventral caudal process of that genus.

Remarks. This species raises considerable problems in its generic placement as is obvious from the diagnosis. Apart from the lack of a sharp caudal process and in consequence the more uniform height, the other features all fit well within that genus. It has not been possible to find anything closely comparable to this species.

Genus SCHIZOCYTHERE Triebel, 1950
Schizocythere deopanica sp. nov.

Plate 43, figs. 6–9, 11

Holotype. Female carapace IPE/H02/03/920.

Paratypes. Four carapaces IPE/P02/03/921–924.

Other material. Thirty specimens from DP11, two specimens from DP8.

Type horizon. DP11.

Derivation of name. After the Deopani River area of Assam where the material was collected.

EXPLANATION OF PLATE 43

Figs. 1–3. *Paijenborchella* (*Eopaijenborchella*) *assamensis* sp. nov. All from sample DP8. 1, female carapace in ventral view, paratype, IPE/P02/03/997, × 132. 2, male carapace in ventral view, paratype, IPE/P02/03/998, × 148. 3, male carapace in dorsal view, paratype, IPE/P02/03/999, × 114.

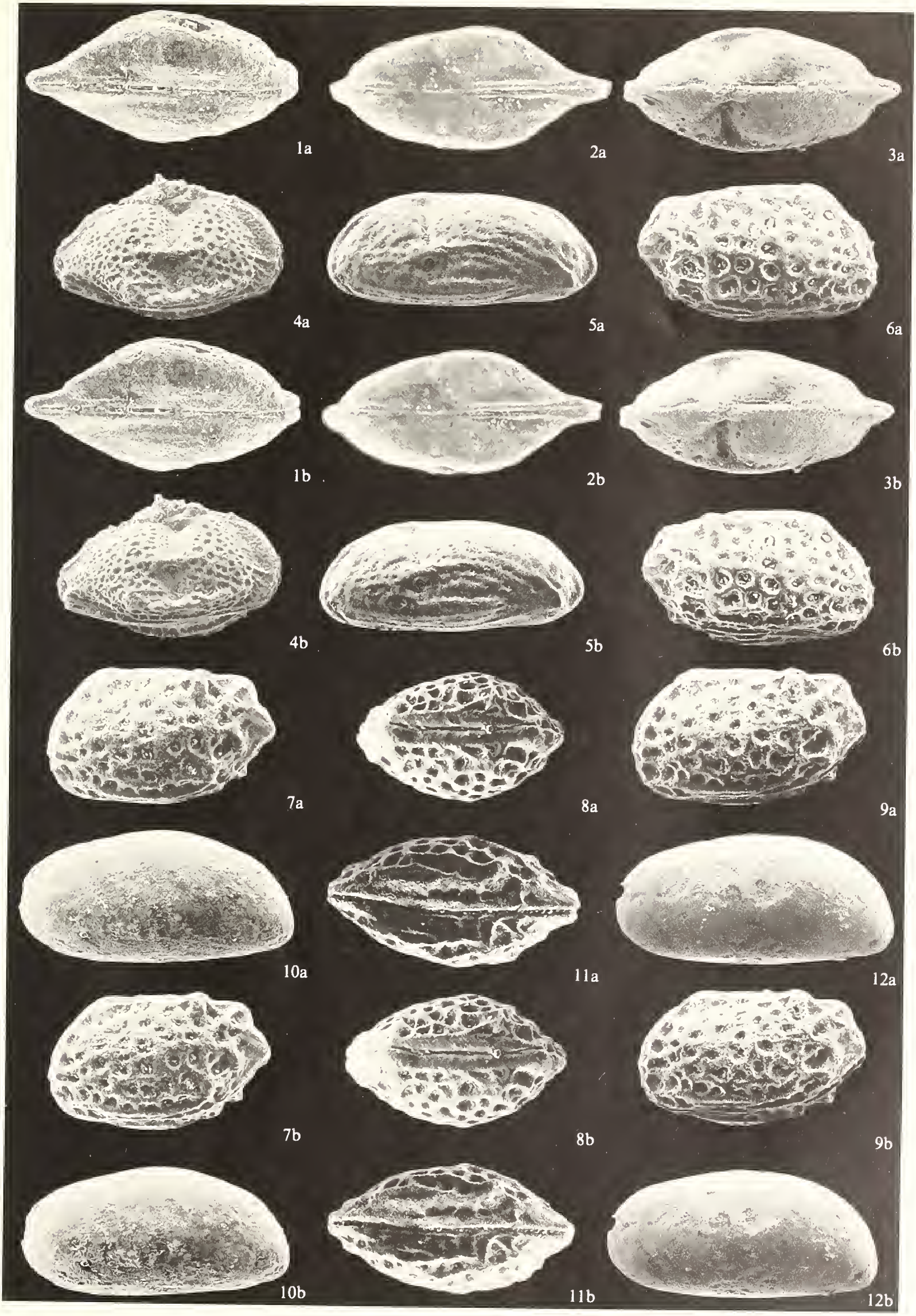
Fig. 4. *Paijenborchella* sp., female carapace from right, IPE/B02/03/954, DP8, × 103.

Fig. 5. *Paijenborchella? enigma* sp. nov., carapace from left, IPE/H02/03/971, DP6, × 85.

Figs. 6–9, 11. *Schizocythere deopanica* sp. nov. All from sample DP11. 6, female carapace from right, holotype, IPE/H02/03/920, × 98. 7, female carapace from left, paratype, IPE/P02/03/922, × 95. 8, female carapace in dorsal view, paratype, IPE/P02/03/923, × 95. 9, male carapace from left, paratype, IPE/P02/03/921, × 93. 11. male carapace in dorsal view, paratype, IPE/P02/03/924, × 100.

Figs. 10, 12. *Krithe oryza* sp. nov. All from sample DP11. 10, female carapace from left, paratype, IPE/P02/03/1001, × 105. 12, male carapace from left, paratype, IPE/P02/03/1005, × 82.

PLATE 43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NEALE and SINGH, *Paijenborchella*, *Schizocythere*, *Krithe*

Dimensions of figured specimens.

	Length	Height	Width
Holotype, female carapace, IPE/H02/03/920	400 μm	240 μm	210 μm
Paratype, female carapace, IPE/P02/03/923	420 μm	255 μm	220 μm
Paratype, male carapace, IPE/P02/03/921	410 μm	250 μm	220 μm
Paratype, female carapace, IPE/P02/03/922	400 μm	255 μm	230 μm
Paratype, male carapace, IPE/P02/03/924	410 μm	255 μm	220 μm

Diagnosis. A species whose strong reticulate ornamentation includes a strong posterodorsal tubercle with a rib from its posterior slope to the posterodorsal corner.

Remarks. This species shows the usual, heavily reticulate carapace typical of the genus, a genus widely recorded from throughout the northern hemisphere in beds of Eocene to Miocene age. It is very close to *S. gujaratensis* Guha, 1968 which has been well figured by Siddiqui (1981) who found it in the middle upper Eocene of the Zao River Section in the Sulaiman Range, Pakistan. The present species is very close in possessing a similar posterodorsal tubercle but differs consistently in the presence of a rib from the posterior slope of this to the posterodorsal corner of the valve. The anterodorsal part of the valve is also less excavated and there are differences in the detailed arrangement of the fossae where the diagonal alignment across the shell does not depart so strongly from the horizontal. Its close similarity to the western species from Kutch and the Sulaiman Range suggest that it is of similar Eocene age.

Other species placed in *Schizocythere* are not closely comparable.

Family CUSHMANIDEIDAE Puri, 1973
Genus CUSHMANIDEA Blake, 1933
Cushmanidea distincta sp. nov.

Plate 46, fig. 11

Holotype. Carapace IPE/H02/03/976

Horizon. DP8

Derivation of name. From its easily recognized appearance.

Dimensions of figured specimen.

	Length	Height	Width
Holotype, carapace, IPE/H02/03/976	512 μm	164 μm	156 μm

Diagnosis. A slightly boomerang-shaped species of *Cushmanidea* which is very long in proportion to height where the ratio is more than three to one.

Remarks. Cushmanidea is not a commonly encountered genus and *C. tewarii* Khosla, 1972 from the Eocene of Rajasthan appears to be the only other record from the Tertiary of the Indian subcontinent. Whilst represented by only one specimen the present form is sufficiently distinctive to warrant a name rather than leaving it under open nomenclature.

Family KRITHIDAE MANDELSTAM, 1960
Genus KRITHE Brady, Crosskey and Robertson, 1874
Krithe oryza sp. nov.

Plate 43, figs. 10, 12; Plate 46, fig. 13

Holotype. Carapace IPE/H02/03/925.

Paratypes. Carapaces IPE/P02/03/1001, 1005.

Type horizon. DP11.

Derivation of name. Greek *Oryza*, 'rice', from its resemblance to a grain of rice.

Dimensions of figured specimens.

	Length	Height	Width
Holotype, male carapace, IPE/H02/03/925	540 μm	270 μm	250 μm
Paratype, female carapace, IPE/P02/03/1001	430 μm	225 μm	210 μm
Paratype, male carapace, IPE/P02/03/1005	555 μm	270 μm	250 μm

Diagnosis. A species almost exactly half as high as long with gently convex ventral outline and gently convex dorsal outline. Greatest height in the male lies at approximately three-quarters the length, in the female just posterior of mid-length.

Remarks. Because all the material consists of closed carapaces it has not been possible to ascertain the nature of the hinge and thus whether it should be placed in *Krithe* or *Dentokrithe* Khosla and Haskins, 1980 (type species *Krithe indica* Tewari and Tandon, 1960 from the middle Eocene of Western India). From this latter species *K. oryza* differs in the more vaulted dorsal margin and in the somewhat narrower anterior part of the valve as seen in lateral view. The differences are perhaps most clearly seen, however, in the even rounding of the anterior margin of *K. oryza* in side view compared with the infracurvature of *D. indica.* The ventral margin is also more convex in the present species. Differences from the Indian Miocene *D. autochthona* (Lubimova and Guha) are obvious and seen in the concave ventral margin and well-developed posterodorsal region with almost vertical posterior margin of the Miocene form.

Krithe cf. *K. oryza*

Plate 44, fig. 1

Material. A single carapace IPE/B02/03/977.

Type horizon. DP8.

Dimensions of figured specimen.

	Length	Height	Width
Carapace IPE/B02/03/977	448 μm	220 μm	220 μm

Remarks. This specimen occurred *c.*12 m (40 feet) lower in the section than *K. oryza.* It compares closely with the female of the last species which it resembles in size but shows slight differences in shape with anterior and posterior ends being a little more narrowly rounded in side view and the antero- and posterodorsal margins a little straighter. Lacking a full range of material from DP8 it is not possible to place the present form unequivocally in *K. oryza* and so here the question is left open.

Family TRACHYLEBERIDIDAE Sylvester-Bradley, 1948
Subfamily TRACHYLEBERIDINAE Sylvester-Bradley, 1948
Tribe ECHINOCYTHEREIDINI Hazel, 1967
Genus ALOCOPOCYTHERE Siddiqui, 1971
Alocopocythere bhandarii sp. nov.

Plate 44, figs. 2–4

Holotype. Carapace IPE/H02/03/957.

Paratypes. Six other specimens from the same sample.

Type horizon. DP8.

Derivation of name. In honour of Sri L. L. Bhandari, Director of the Keshava Deva Malaviya Institute of Petroleum Exploration, O.N.G. Commission, Dehra Dun.

Dimensions of figured specimens.

	Length	Height	Width
Holotype, male carapace, IPE/H02/03/957	640 μm	340 μm	330 μm
Paratype, female carapace, IPE/P02/03/955	550 μm	320 μm	330 μm
Paratype, female carapace, IPE/P02/03/958	560 μm	340 μm	325 μm

Diagnosis. Carapace strongly pitted but with the anterior marginal rim smooth or only faintly ribbed. Just behind mid-length a short, distinctive rib starts at about one-quarter height and runs upwards and slightly posteriorly to about mid-height.

Remarks. A considerable number of *Alocopocythere* species has been described from early Tertiary rocks of the western India/Pakistan/Saudi Arabia area but none is closely comparable with the present species and its distinct ornamentation.

Alocopocythere dhansariensis sp. nov.

Plate 44, figs. 5–7, 9

Holotype. Male carapace IPE/H02/03/962.

Paratypes. Eighty-three specimens from Horizon DP8 including IPE/P02/03/960, 961, 963.

Other material. Thirteen specimens from DP11.

Type horizon. DP8.

Derivation of name. After the Dhansari Valley where the specimens were collected.

Dimensions of figured specimens.

	Length	Height	Width
Holotype, male carapace, IPE/H02/03/962	530 μm	250 μm	220 μm
Paratype, female carapace, IPE/P02/03/960	450 μm	245 μm	230 μm
Paratype, female carapace, IPE/P02/03/963	470 μm	260 μm	240 μm
Paratype, male carapace, IPE/P02/03/961	510 μm	240 μm	220 μm

Diagnosis. An elongate species with well-developed marginal pits all round the carapace of which seven are present on the anterior marginal rim. Prominent surface pitting which tends to be smoothed out in the posteroventral part of the valve.

Remarks. Other species are not close. The closest comparison is to be found among the Pakistan material where the male of *A. rupina* Siddiqui, 1971 is close in shape to the female of the present species but differs in ornamentation and shape in dorsal view as well as in the different dimorphism.

EXPLANATION OF PLATE 44

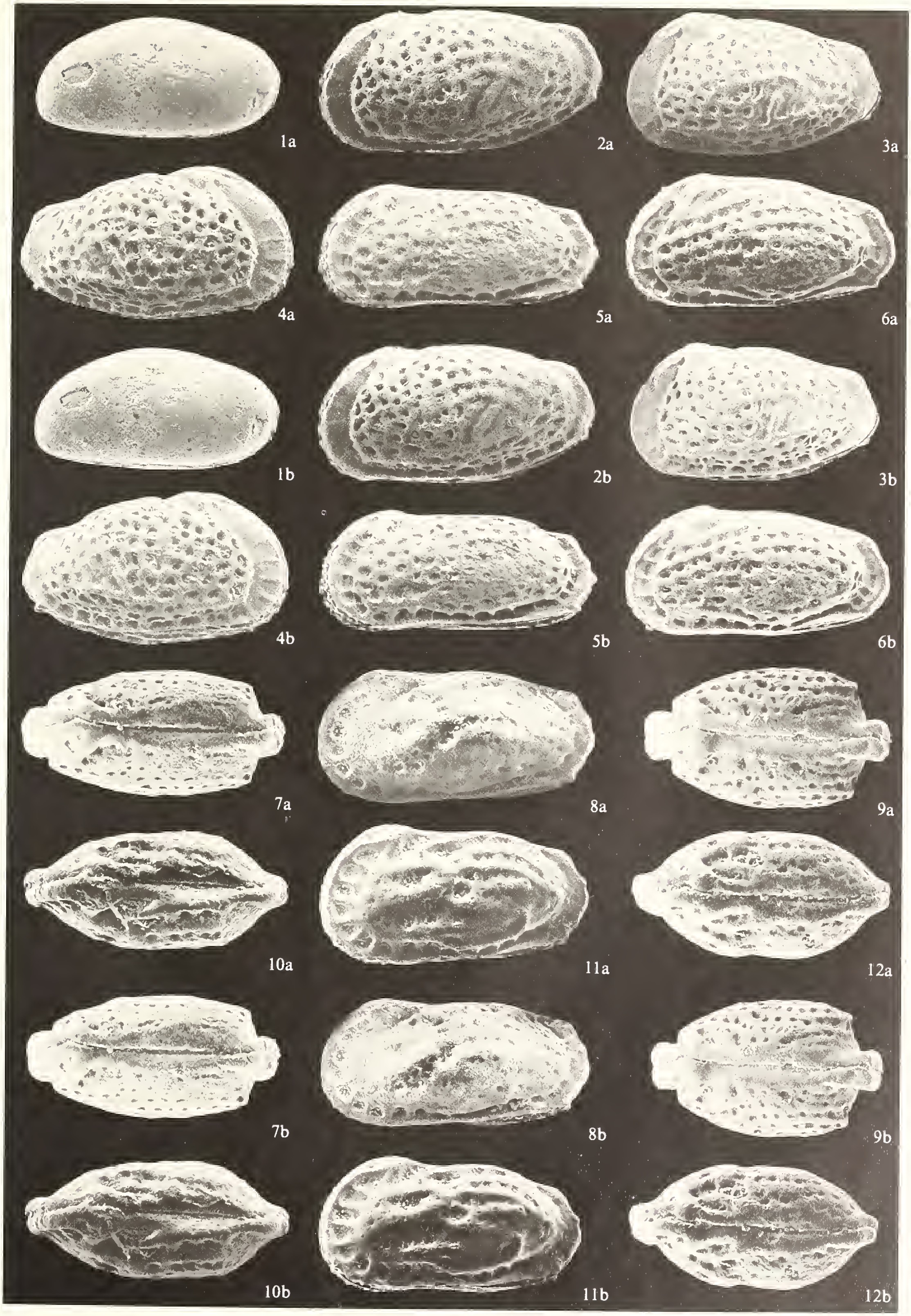
Fig. 1. *Krithe* cf. *K. oryza*, carapace from left, IPE/B02/03/977, DP8, ×89.

Figs. 2–4. *Alocopocythere bhandarii* sp. nov. All from sample DP8. 2, male carapace from left, holotype, IPE/H02/03/957, ×73. 3, female carapace from left, paratype, IPE/P02/03/958, ×75. 4, female carapace from right, paratype, IPE/P02/03/955, ×82.

Figs. 5–7, 9. *Alocopocythere dhansariensis* sp. nov. All from sample DP8. 5, male carapace from left, holotype, IPE/H02/03/962, ×87. 6, female carapace from left, paratype, IPE/P02/03/960, ×98. 7, male carapace in dorsal view, paratype, IPE/P02/03/963, ×86. 9, female carapace in dorsal view, paratype, IPE/P02/03/961, ×74.

Figs. 8, 10–12. *Alocopocythere talukdari* sp. nov. All from sample DP11. 8, male carapace from left, holotype, IPE/H02/03/934, ×82. 10, male carapace in dorsal view, paratype, IPE/P02/03/935, ×83. 11, female carapace from left, paratype, IPE/P02/03/933, ×86. 12, female carapace in dorsal view, paratype, IPE/P02/03/937, ×77.

PLATE 44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NEALE and SINGH, *Krithe*, *Alocopocythere*

Alocopocythere talukdari sp. nov.

Plate 44, figs. 8, 10–12

Holotype. Male carapace IPE/H02/03/934.

Paratypes. One male and two female carapaces IPE/P02/03/935, 933, 937.

Type horizon. DP11.

Derivation of name. In honour of Sri Samrendra Nath Talukdar, Member Exploration, O.N.G. Commission, Dehra Dun.

Dimensions of figured specimens.

	Length	Height	Width
Holotype, male carapace, IPE/H02/03/934	550 μm	280 μm	255 μm
Paratype, female carapace, IPE/P02/03/933	510 μm	290 μm	255 μm
Paratype, male carapace, IPE/P02/03/935	520 μm	300 μm	245 μm
Paratype, female carapace, IPE/P02/03/937	530 μm	280 μm	240 μm

Diagnosis. Carapace with well-developed marginal pits and with the pits on the general surface of the valve subdued at the expense of the ribbing developed between them. Dorsal margin in side view gently triconvex.

Remarks. The only species resembling this is *A. orectommata* Al-Furaih, 1980 from the Palaeocene of Saudi Arabia but this differs in the less inflated ribbing and in the detailed rib pattern in the anterodorsal region of the valve.

Alocopocythere polygona sp. nov.

Plate 45, figs. 1–3

Holotype. Male carapace IPE/H02/03/987.

Paratypes. Two female carapaces IPE/P02/03/984, 988.

Horizon. DP13.

Derivation of name. A reference to the polygonal shape of the surface pitting.

Dimensions of figured specimens.

	Length	Height	Width
Holotype, male carapace, IPE/H02/03/987	568 μm	330 μm	304 μm
Paratype, female carapace, IPE/P02/03/984	540 μm	310 μm	300 μm
Paratype, female carapace, IPE/P02/03/988	640 μm	352 μm	356 μm

Diagnosis. A species with rather smooth anterior and posterior marginal areas and polygonal pitting on the valve surface. Female very rotund in dorsal view.

Remarks. There is little in the literature with which this can be compared although *A. transversa* Morphotype F described by Siddiqui (1971) from the upper Eocene of the Rakhi Nala Section of Pakistan has a number of features reminiscent of the present species. However, the marginal rim in his Morphotype shows strong pitting anteriorly and posteriorly and the ventral margin lacks the even, elegant curve of the present species.

Subfamily BUNTONIINAE Apostolescu, 1961
Genus BUNTONIA Howe, 1935
Buntonia royi sp. nov.

Plate 45, figs. 4–7

Holotype. Male carapace IPE/H02/03/968.

Paratypes. Female carapace IPE/P02/03/969.

Type horizon. DP6.

Other horizons. DP8, including figured specimens IPE/B02/03/980, 982.

Derivation of name. In honour of Sri T. K. Roy, Superintending Geologist, K.D.M.I.P.E., O.N.G.C., who contributed much to our understanding of the geology of the Assam Region.

Dimensions of figured specimens.

	Length	Height	Width
Holotype, male carapace, IPE/H02/03/968	410 μm	215 μm	180 μm
Paratype, female carapace, IPE/P02/03/969	390 μm	240 μm	180 μm
Male carapace IPE/B02/03/980	400 μm	220 μm	164 μm
Male carapace IPE/B02/03/982	336 μm	236 μm	196 μm

Diagnosis. A species with well-developed pitting dominating over subdued ribbing and dorsally directed termination of the posterior margin.

Remarks. The present species differs from *B. awadi* Bassiouni, 1969 from the Eocene of Jordan in which the ventral part of the valve shows a characteristic bulge/overhang and the dorsal margin is slightly concave or undulating.

Family LOXOCONCHIDAE Sars, 1925
Genus LOXOCONCHA Sars, 1866
Loxoconcha? sp.

Plate 46, fig. 6

A single specimen which appears to belong in this genus but in which the caudal process is much drawn out.

Horizon. DP8.

Dimensions of figured specimen.

	Length	Height	Width
Carapace IPE/X02/03/983	276 μm	152 μm	144 μm

Remarks. This single specimen has a narrower and more pronounced caudal process than that found in most members of the genus although forms of comparable shape have been illustrated. *Loxoconcha* is typical of shallow shelf seas and is not normally recorded in this part of Tethys. This carapace is very small compared with most species and although showing distinctive and well-developed ornamentation there must remain some doubt about whether it is a full adult and actually lived in the place where it was found. For this reason it is left under open nomenclature.

Family PARACYTHERIDEIDAE Puri, 1957
Genus PARACYTHERIDEA G. W. Muller, 1894
Paracytheridea? superdimorphica sp. nov.

Plate 45, figs. 8–10

Holotype. A male carapace IPE/H02/03/966.

Paratypes. A male and a female carapace IPE/P02/03/965, 967.

Type horizon. DP8.

Derivation of name. In reference to the extraordinary dimorphism seen in this species as interpreted here.

Dimensions of figured specimens.

	Length	Height	Width
Holotype, male carapace, IPE/H02/03/966	380 μm	170 μm	155 μm
Paratype, female carapace, IPE/P02/03/965	330 μm	180 μm	140 μm
Paratype, male carapace, IPE/P02/03/967	350 μm	170 μm	155 μm

Diagnosis. A species in which four ribs radiate from the anteroventral corner. One runs to the anterior cardinal angle. Two lie ventrally, the upper one being discontinuous and forming the boundary between the ventral and lateral surface. A median rib runs to the posterodorsal corner. The median rib disappears at the median sulcus and reappears posteriorly as a short double rib. In the female this part is elevated to form a strong tubercle which affects the dorsal outline in side view.

Remarks. This material has been placed provisionally in the genus *Paracytheridea* to which it has certain affinities although it most certainly does not belong there. Unfortunately all the material consists of closed carapaces and it is impossible to determine the hinge structure and other features necessary to establish a new genus. Interpretation, based on three specimens from the same horizon, was also difficult at the specific level. Two of the specimens differ greatly in shape from the third but in all of them the anterior half of the valve is very similar. The posterior half, however, shows very marked differences in that the higher form has the dorsoposterior area of ornamentation raised to form a strong tubercle which affects the dorsal outline of the shell in side view (Pl. 45, fig. 9). In the same area the lower, more elongate form has ridges in a low inverted 'V' which appear to represent the same elements but are not raised to form a marked tubercle. Detailed examination of Pl. 45, figs. 9, 10 will show other differences such as the greater inflation of the upper ventral rib in the higher form. Since these are all from the same sample, the latter is interpreted as a female and the lower forms are interpreted as males, one of which is selected as the holotype. There is nothing described from the Indian sub-continent which is closely comparable with the present species.

Family CYTHERURIDAE G. W. Muller, 1894
Subfamily CYTHERURINAE G. W. Muller, 1894
Genus CYTHERURA Sars, 1866
Cytherura eocaenica sp. nov.

Plate 46, fig. 10

Holotype. Carapace IPE/H02/03/947.

Type Horizon. DP11.

Derivation of name. From its occurrence in the Eocene.

Dimensions of figured specimen.

	Length	Height	Width
Holotype, carapace, IPE/H02/03/947	390 μm	150 μm	110 μm

Diagnosis. An elongate species with well-developed dorsocentral and ventrocentral longitudinal ribs which run the length of the valves. Between these two ribs there are two strong, short longitudinal ribs

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EXPLANATION OF PLATE 45

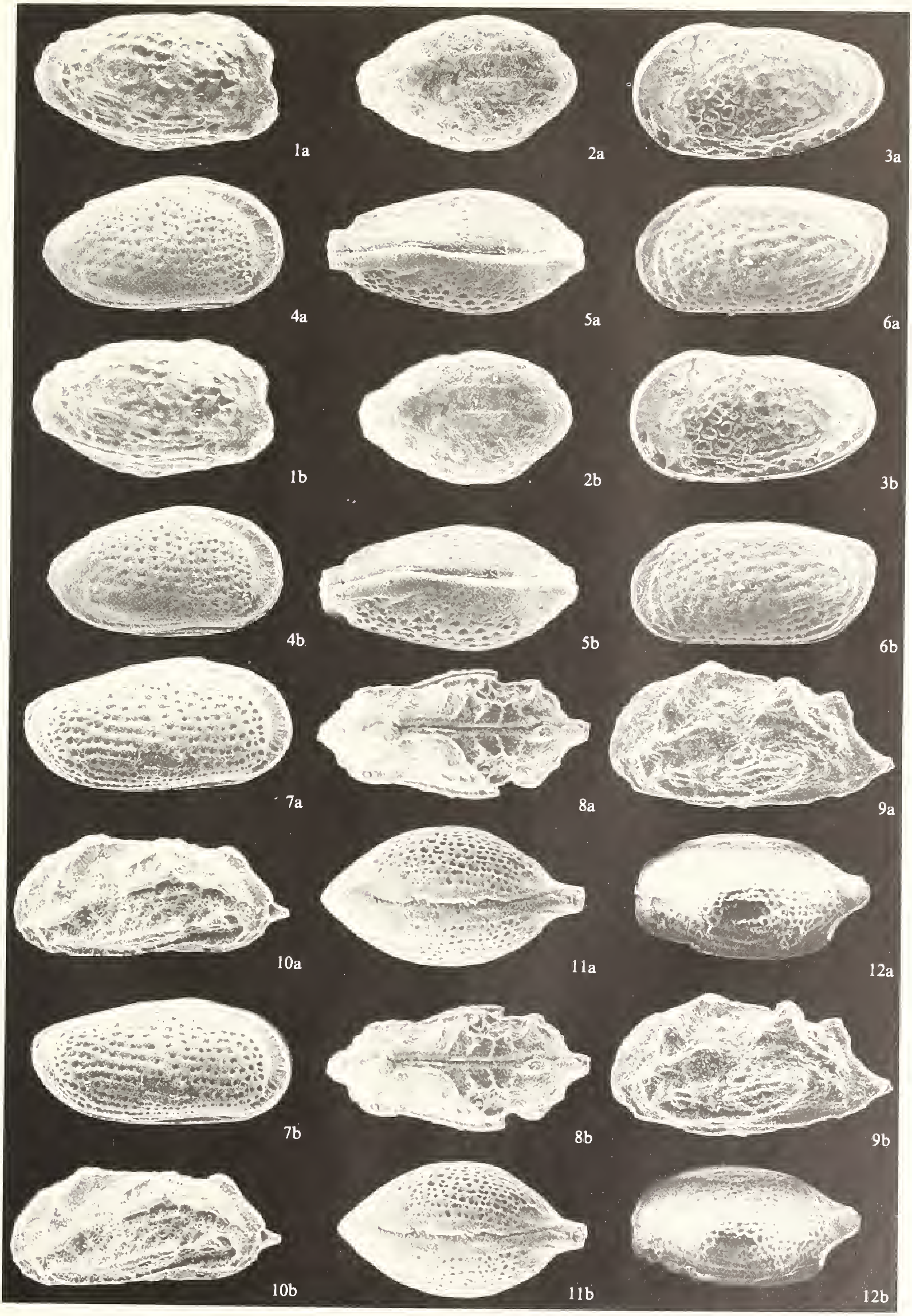
Figs. 1–3. *Alocopocythere polygona* sp. nov. All from sample DP13. 1, female carapace from right, paratype, IPE/P02/03/984, × 74. 2, female carapace in dorsal view, paratype, IPE/P02/03/988, × 58. 3, male carapace from left, holotype, IPE/H02/03/987, × 73.

Figs. 4–7. *Buntonia royi* sp. nov. 4, female carapace from right, paratype, IPE/P02/03/969, DP6, × 103. 5, male carapace in dorsal view, IPE/B02/03/982, DP8, × 125. 6, male carapace from left, holotype, IPE/H02/03/968, DP6, × 100. 7, male carapace from right, IPE/B02/03/980, DP8, × 110.

Figs. 8–10. *Paracytheridea*? *superdimorphica* sp. nov. All from sample DP8. 8, male carapace in dorsal view, paratype, IPE/P02/03/967, × 126. 9, female carapace from left, paratype, IPE/P02/03/965, × 142. 10, male carapace from left, holotype, IPE/H02/03/966, × 118.

Figs. 11, 12. *Semicytherura indica* sp. nov. All from sample DP11. 11, carapace in dorsal view, paratype, IPE/P02/03/917, × 119. 12, carapace from left, paratype, IPE/P02/03/916. × 105.

PLATE 45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NEALE and SINGH, *Eocene Ostracoda*

in the anterior fifth of the valves which also join the anterior margin. About nine other finer longitudinal ribs occur on the lateral surface of which three lie between the two stronger ribs. The posterior end of the carapace is marked off from the main body of the valve and is reticulate and immediately behind the anterior rim the valve is strongly depressed between the ribs.

Remarks. This single specimen is so distinctive and so well preserved that it is unlikely to be confused with any other taxon and is therefore named. It has not been possible to determine hinge structure, nature of marginal areas, or muscle scar pattern and it is here referred to *Cytherura* on the basis of its general shape, both the elongation and particularly the posterior outline in side view being reminiscent of that genus. The dominantly longitudinal ornamentation, however, is more typical of *Semicytherura* than the present day species of *Cytherura*. When more, well-preserved material is available it may be necessary to re-consider the generic placement of this taxon.

Genus SEMICYTHERURA Wagner, 1957

Semicytherura indica sp. nov.

Plate 45, figs. 11, 12; Plate 46, figs. 1, 3

Holotype. Carapace IPE/H02/03/915.

Paratypes. Three carapaces IPE/P02/03/916, 917, 994.

Type horizon. DP11.

Derivation of name. From its occurrence in the Indian sub-continent.

Dimensions of figured specimens.

	Length	Height	Width
Holotype, carapace, IPE/H02/03/915	370 μm	200 μm	180 μm
Paratype, carapace, IPE/P02/03/917	360 μm	200 μm	180 μm
Paratype, carapace, IPE/P02/03/916	370 μm	210 μm	200 μm
Paratype, carapace, IPE/P02/03/994	330 μm	210 μm	185 μm (broken)

Diagnosis. A finely reticulate species in which the individual lines of fossae are separated by fine longitudinal ribs which number about eighteen on the main body of the valve.

Remarks. As only closed carapaces were available for study this species is provisionally placed in *Semicytherura* on the basis of the curved dorsal margin rather than in *Cytherura* where the type species is very different and has a straight dorsal margin. Nevertheless, when good material showing

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EXPLANATION OF PLATE 46

Figs. 1, 3. *Semicytherura indica* sp. nov. Both from DP11. 1, carapace from right, holotype. IPE/H02/03/915, × 105. 3, carapace from left, paratype, IPE/P02/03/994, × 118.

Fig. 2. *Semicytherura indica* sp. nov. ?subsp. nov., carapace from right, IPE/B02/03/1017, DP13, × 125.

Figs. 4, 5. *Cytheropteron reticuloradiata* sp. nov. 4, carapace from right, holotype, IPE/H02/03/973, DP8, × 106. 5, carapace from left, IPE/B02/03/995, DP11, × 134.

Fig. 6. *Loxoconcha*? sp., carapace from left, IPE/X02/03/983, DP8, × 156.

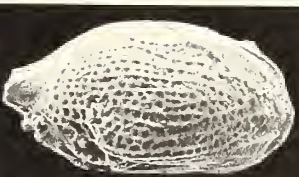
Figs. 7–9. *Uroleberis armeniaca* sp. nov. 7, female carapace from right, IPE/B02/03/913, DP11, × 88. 8, female carapace in dorsal view, IPE/B02/03/914, DP11, × 85. 9, male carapace from right, holotype, IPE/H02/03/275, DP13, × 86.

Fig. 10. *Cytherura eocaenica* sp. nov., carapace from right, holotype, IPE/H02/03/947, DP11, × 115.

Fig. 11. *Cushmanidea distincta* sp. nov., carapace from right, holotype, IPE/H02/03/976, DP8, × 88.

Fig. 12. *Xestoleberis*? sp., carapace from right, IPE/X02/03/1016, DP8, × 167.

Fig. 13. *Krithe oryza* sp. nov., carapace from right, holotype, IPE/H02/03/925, DP11, × 80.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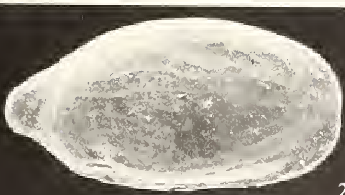
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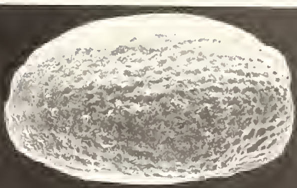
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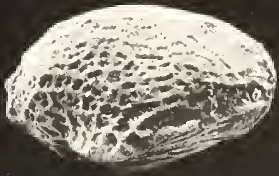
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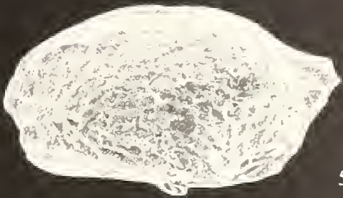
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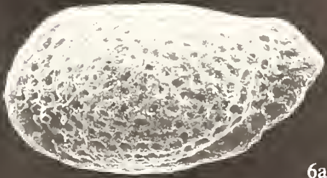
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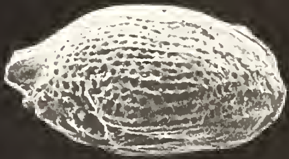
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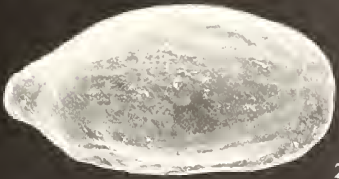
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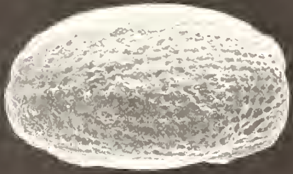
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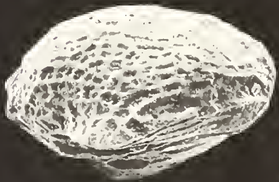
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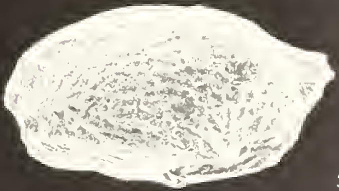
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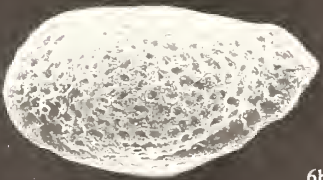
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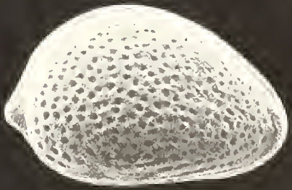
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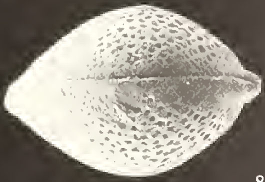
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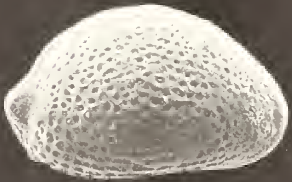
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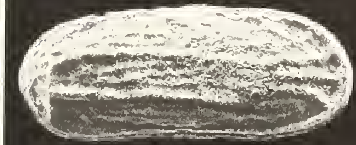
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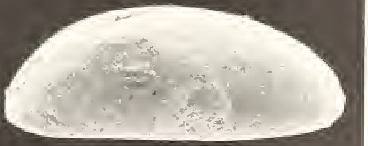
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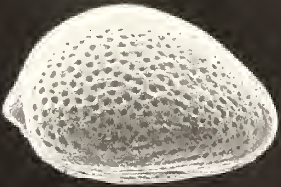
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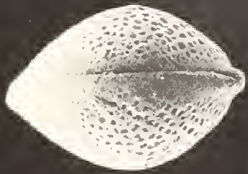
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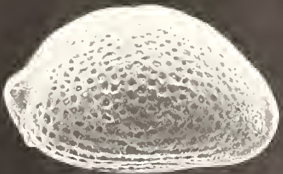
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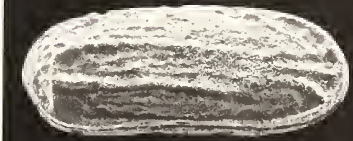
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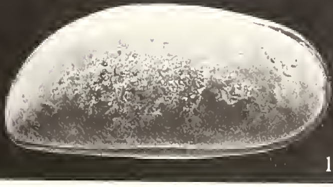
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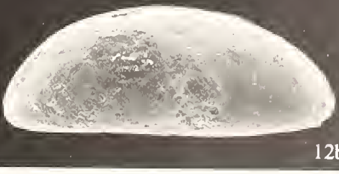
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NEALE and SINGH, *Eocene Ostracoda*

the internal features on which the generic differences are essentially drawn become available, it may be necessary to transfer this species to another genus of the Cytheruridae. The closest comparable species appears to be that from the lower Palaeocene of Saudi Arabia recorded as *Semicytherura* sp. by Al-Furaih (1980). The material figured here is closest to his presumed female dimorph in shape although not generally so vaulted dorsally nor so convex ventrally. The surface ornamentation is not well preserved in Al-Furaih's specimens but fine reticulation and ribbing were present and although the details cannot be made out the general size of the reticules is closely comparable with the Assam species. *S. rameshi* (Singh and Misra), 1968 from the Fuller's Earth (Eocene) of Rajasthan, and described also from the Eocene of Rajasthan by Khosla (1972) with its relatively coarse reticulation and greater alation is not close.

Semicytherura indica sp. nov. ?subsp. nov.

Plate 46, fig. 2

Material. A carapace IPE/B02/03/1017.

Type horizon. DP13.

Dimensions of figured specimen.

	Length	Height	Width
Carapace IPE/B02/03/1017	360 μm	200 μm	160 μm

Remarks. The single specimen comes from Sample DP13 *c*.4.5 m (15 feet) above the sample yielding *S. indica* s.s. The specimen agrees in general shape and in the pattern of the main longitudinal ribs running across the shell. The whole ornamentation is smoothed out, however, although suggestions of fine reticulation are perhaps seen in places. Until more material is found it is impossible to say whether this is merely a phenomenon of preservation or whether this represents a new subspecies which may be useful stratigraphically.

Subfamily CYTHEROPTERINAE Hanai, 1957

Genus CYTHEROPTERON Sars, 1866

Cytheropteron reticuloradiata sp. nov.

Plate 46, figs. 4, 5

Holotype. Carapace IPE/H02/03/973.

Type horizon. DP8.

Other Material. A carapace IPE/B02/03/995 from DP11.

Derivation of name. A reference to the reticulation which appears to radiate from the alae.

Dimensions of figured specimens.

	Length	Height	Width
Holotype. Carapace IPE/H02/03/973	350 μm	235 μm	210 μm
Carapace IPE/B02/03/995	335 μm	210 μm	175 μm

Diagnosis. A reticulate species of *Cytheropteron* in which the longitudinal ribs 'V' down towards the alae and four ribs sweep down to the edge of the ala.

Remarks. In the holotype (Pl. 46, fig. 4) there is the suggestion of a swelling where an eye tubercle would be expected, but careful examination shows that this is not an ocular structure and that the specimen is thus not referable to *Oculocytheropteron* Bate, (1972). The specimen from DP11 occurs *c*.12 m (40 feet) higher in the section and the ornamentation is not so well preserved. The principal elements appear to be identical, however, and at present there is no reason to consider it a different taxon.

Family XESTOLEBERIDIDAE Sars, 1928
Genus UROLEBERIS Triebel, 1958
Uroleberis armeniaca sp. nov.

Plate 46, figs. 7–9

Holotype. Male carapace IPE/H02/03/912.

Other material. Two female carapaces IPE/P02/03/913, 914 from Sample DP11.

Type horizon. DP13.

Derivation of name. Latin *armeniacum*, 'apricot' in reference to its resemblance to an apricot stone.

Dimensions of figured specimens.

	Length	Height	Width
Holotype, male carapace, IPE/H02/03/912	440 μm	295 μm	275 μm
Female carapace, IPE/B02/03/913	445 μm	310 μm	280 μm
Female carapace, IPE/B02/03/914	400 μm	270 μm	240 μm

Diagnosis. A species of *Uroleberis* with short but well-developed caudal process and pitting which becomes finer peripherally. The greatest height lies at approximately two-thirds length and the anterior end is fairly narrowly rounded.

Remarks. Uroleberis is commonly encountered in the Middle Eastern and Indian part of Tethys and a number of species has been described. *U. kutchensis* Guha, 1968 from the middle Eocene of Kutch, and found also by Khosla (1972) in the middle Eocene of Rajasthan, has a very marked posteroventral projection not seen in the Assam species. The same is true of *Uroleberis*? *chamberlaini* Sohn, 1970 from the early Tertiary Meting Limestone of Pakistan. None of the four species from the Palaeocene of Saudi Arabia figured by Al-Furaih (1980) are closely comparable. The two species from the lower Eocene of Tamilnadu by Guha and Shukla (1973) are even further removed.

Xestoleberis? sp.

Plate 46, fig. 12

Horizon. DP8.

Dimensions of figured specimen.

	Length	Height	Width
Carapace IPE/X02/03/1016	270 μm	110 μm	115 μm

Remarks. Information on this single specimen is limited to the general shape and the fact that the left valve appears to be slightly larger than the right. It is similar to some of the more elongate species of *Xestoleberis*, especially the male dimorphs, and it is here provisionally referred to that genus pending further information.

FAUNAL COMPARISONS

The closest comparable faunas are those described from the Eocene of western India and Pakistan over a thousand miles away. Generic similarity is close as seen in the presence of *Cytherella*, *Cytherelloidea*, *Bairdia*, *Paijenborchella*, *Schizocythere*, *Alocopocythere*, *Semicytherura*, *Krithe*, *Uroleberis*, and *Xestoleberis* in both areas. These largely cosmopolitan genera confirm that there is no isolation of the Assam area at the generic level of development. There is almost no correspondence at the specific level, however, which consequently may be regarded as due principally to geographical distance from other known faunas. The incidence of generic representation also shows some differences.

The Platycopina are very well developed in the Eocene of Assam where eight species have been recognized although two are rare and not well enough known to be named. In general this group tends to be neglected since recognition is dependent on few morphological parameters and so many authors restrict their studies to the Podocopina. However, three species have been described from western India but none of these are seen in Assam. Here the *Cytherella* fauna is not closely comparable with any hitherto described Eocene fauna although in certain cases there is some resemblance to species described from Argentina, Nigeria, and New Zealand. The genus *Cytherella* gives the impression of being much better developed and much more diverse than elsewhere in the sub-continent and forms a higher proportion of the fauna. On the other hand *Cytherelloidea* is rare, a feature reflected in the faunas from other comparable areas during the Eocene. Unlike the Eocene of western India, *Bairdia* does not form a large element in the fauna and the single species is referred to *B. beraguaensis* and is the only one common to this area and western India.

As in western India and Pakistan the cytheracean genera *Alocopocythere*, *Schizocythere*, *Paijenborchella*, and *Uroleberis* are well represented albeit by different species. In contrast spinose and tuberculate forms such as *Trachyleberis* and *Actinocythereis* together with genera such as *Stigmatocythere* and *Occultocythereis* are absent. Finally the Cytheruridae, although still not common, appear to be much better represented than in western India although this may be simply a matter of collection failure in the latter area.

Palaeoecologically, it is clear that the fauna is fully marine. *Cytherelloidea*, although rare, is present, a fact which together with the larger benthonic Foraminifera suggests a warm sea with a year-round temperature which did not fall below about 11 °C. Depth is more difficult to assess accurately. Clearly the fauna is not littoral or abyssal. *Cytherella*, which forms such an important element in the fauna, ranges over a wide range of depths at the present day from shallow, even brackish, environments to bathyal and even abyssal depths. In the latter habitats the genus is usually represented by large, smooth species. Here the high incidence of punctate forms is more in accord with an inner shelf locale. This is supported by the occurrence of *Alocopocythere* which is still extant and ranges from the Red Sea and Persian Gulf to Western Australia (Siddiqui, 1983). Typically, it lives in shallow marine areas from the eulittoral down to about 200 metres. Negative evidence is provided by the absence of delicately spined or blind Trachyleberidae and a lack of planktonic Foraminifera. Thus the general aspect of the fauna suggests that it is a relatively shallow water shelf fauna.

STRATIGRAPHIC SUCCESSION OF FAUNAS

Detailed study of the ostracod faunas from the middle Eocene Sylhet Formation reveals a striking biostratigraphical succession of faunas (text-fig. 3). One of the most distinctive elements in the fauna is the genus *Alocopocythere* which in the early Tertiary is known to range from Arabia to Assam and to extend more widely later. This genus evolves rapidly and in consequence its species have a relatively short range in time which makes them invaluable biostratigraphical indicators. They have proved particularly useful in this respect in western India and Pakistan (see Siddiqui 1983). Conveniently, each of the Assam faunas contains a unique species of *Alocopocythere* which is used to designate them. The following divisions are recognized:

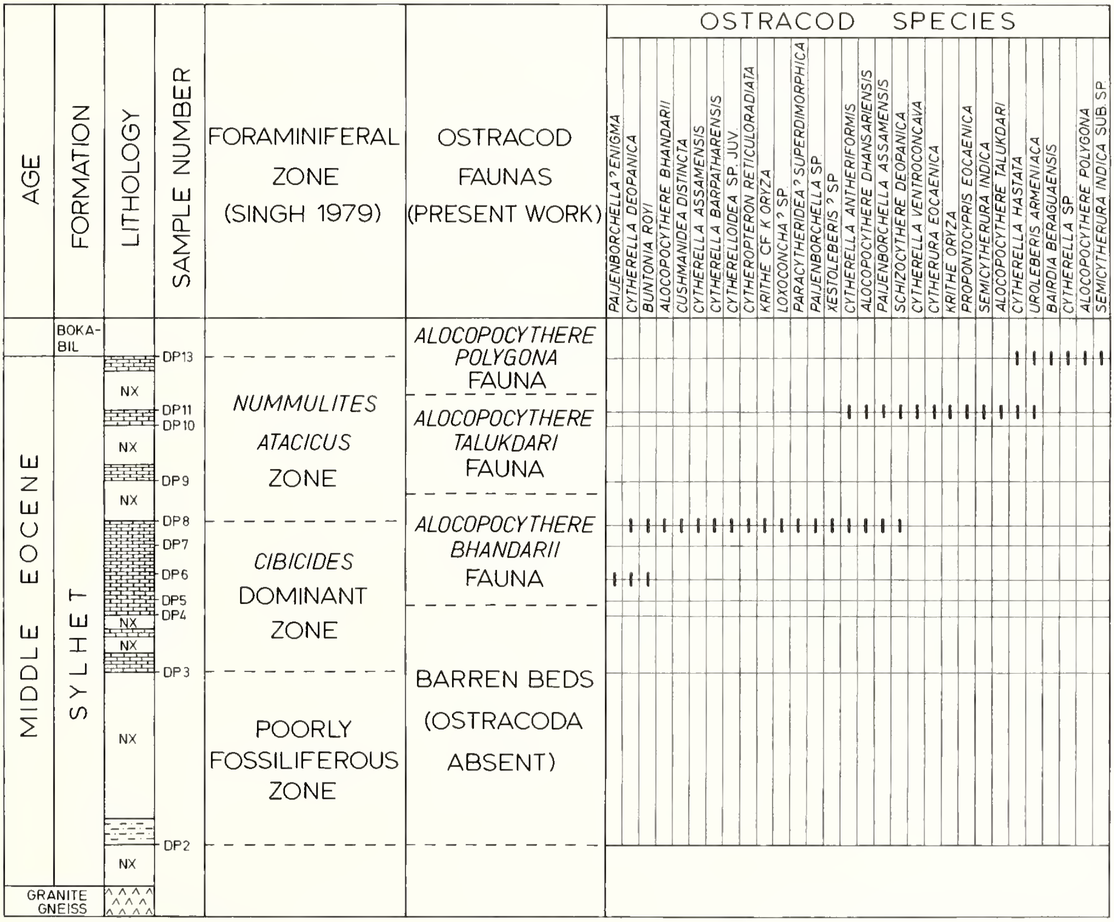
1. Barren Beds. Ostracods have not been obtained so far from some 82 m (270 feet) of beds below the first recorded fauna even though Foraminifera occur in some of the beds. The presence of Foraminifera suggests that ostracods should be present, even if rare, and every opportunity should be taken to carry out further collecting in this part of the section.

2. The *Alocopocythere bhandarii* Fauna. This is found in DP6 and DP8 and thus extends over at least 2 metres (6 feet) of strata. The earliest development in DP6 is small with only three species of which only the rare *Paijenborchella*? *enigma* is confined to that horizon. *Cytherella deopanica* and *Buntonia royi* both occur in DP8 along with the rest of the typical fauna. Sample DP7, collected between DP6 and DP8, consisted of hard limestone from which it was impossible to extract ostracods. However, about 2 m (6 feet) above DP6, sample DP8 yielded a good fauna of seventeen species of which *Alocopocythere bhandarii* is chosen as nominate species. Besides the three species

already named other species found only in DP8 are *Cytherella distincta*, *C. assamensis*, *C. barpatharensis*, *Cytherelloidea* sp. juv., *Cytheropteron reticuloradiata*, *Krithe* cf. *K. oryza*, *Loxoconcha*? sp., *Paijenborchella* sp., *Paracytheridea*? *superdimorphica*, and *Xestoleberis*? sp. In addition *Cytherella antheriformis*, *Alocopocythere dhansariensis*, *Paijenborchella assamensis*, and *Schizocythere deopanica* occur here and also range up into the overlying assemblage.

3. The *Alocopocythere talukdari* Fauna. Named after *A. talukdari* which only occurs here, this fauna is found in material collected from DP11 which lies 10–12 m (35–40 feet) above DP8. Samples DP9 and DP10 collected between here and the previous fauna in DP8 were hard, intractable limestones from which no specimens could be extracted. In addition to the four species ranging up from below, there are five species not found outside this horizon, namely *Cytherella ventroconcava*, *Cytherura eocaenica*, *Krithe oryza*, *Propontocypris eocaenica*, and *Semicytherura indica*. Two species, namely *Cytherella hastata* and *Uroleberis armeniaca* range up into the overlying assemblage.

4. The *Alocopocythere polygona* Fauna. This was found in Sample DP13 lying 1·5–3 m (5–10 feet) above DP11. Besides the two species ranging up from below and the nominate species, three other forms occur here, namely *Bairdia beraguaensis*, what is thought to be a new subspecies of *Semicytherura indica*, and *Cytherella* sp.



TEXT-FIG. 3. Distribution of Ostracoda in the Deopani Traverse. For lithologies, thicknesses, and positions of samples see text-fig. 2.

DISCUSSION

The three faunas are quite distinct but are obviously based on limited samples from a single traverse. For this reason they are here treated as successive faunas rather than as zones or assemblage zones. When further work on boreholes and at outcrop has confirmed the picture obtained in the Deopani Traverse they may be raised to full zonal status.

These faunas cover the foraminiferal zones of '*Cibicides* Dominant' below and '*Nummulites atacicus*' above established by Singh (1979). The only species in common with western India or elsewhere is *Bairdia beraguaensis* which occurs in the Eocene of Jammu and Kashmir State. This precludes any attempt at comparison with the zonal system established in western India.

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BIOTIC DIVERSIFICATION IN THE PHANEROZOIC: DIVERSITY INDEPENDENCE

by ANTONI HOFFMAN

ABSTRACT. The concept of global taxonomic diversity tending to an equilibrium state is central to many macroevolutionary hypotheses. It is widely accepted and considered to be corroborated by quantitative models of biotic diversification in the Phanerozoic. Those models assume diversity dependence of the rates of extinction and origination of taxa. This basic assumption, however, is contradicted by the empirical data. The process of diversification may depend on historical contingencies rather than on general macroevolutionary laws.

THE pattern and process of biotic diversification in the Phanerozoic have been subject to a heated controversy over the last dozen years or so. Rival hypotheses on biotic diversification propose that it is either controlled by extrinsic factors (Valentine 1973), or continues practically limitless (Whittaker 1977), or tends to an equilibrium diversity set by the limits to specialization and to decrease in the average population size (Levinton 1979). A consensus seems to have developed recently that the last hypothesis holds true. In the absence of direct evidence the hypothesis is widely considered to be corroborated by quantitative models of diversification which customarily assume diversity dependence of the rates of origination and extinction of taxa (Sepkoski 1978, 1979; Carr and Kitchell 1980; Kitchell and Carr 1985). These rates are expected to change conversely, or at least to converge, with increasing diversity. Given absence of significant perturbations this would lead to a global equilibrium in diversity. This concept has been central to much macroevolutionary research (Raup *et al.* 1973; Gould *et al.* 1977; Schopf 1979*a*) and it underlies many macroevolutionary hypotheses (Schopf 1974; Simberloff 1974; Bambach 1983; Sepkoski and Sheehan 1983).

The consensus on equilibrium diversity, however, is unwarranted. The models of biotic diversification have not been adequately tested. There are in fact no good empirical data to test any models of evolution of global diversity. Theoretical justifications for those models refer to the species level of the taxonomic hierarchy. Reliable data on global species diversity in the Phanerozoic are beyond the resolution potential of palaeontology, however, at least at the present state of knowledge. Therefore, family level data are widely accepted as the best approximation and customarily applied to macroevolutionary analyses of global diversity.

In the present study I use such data to test the basic assumption of most models of biotic diversification, i.e. the assumption of diversity dependence of taxonomic evolutionary rates. If this assumption is not met, the apparent fit of the models' predictions to the empirical pattern is virtually meaningless.

DATA AND RESULTS

In spite of criticisms (Raup 1972, 1976; Sepkoski 1976; Signor 1978) pointing to severe biases inherent in an early compilation of global diversity in the fossil record (Valentine 1969), an essentially similar compilation by Sepkoski (1982) is widely used as the empirical pattern of taxonomic diversity during the Phanerozoic (Raup and Sepkoski 1982, 1984; Sepkoski and Sheehan 1983; Van Valen 1984; Kitchell and Carr 1985). This is commonly substantiated by the intercorrelation of a number of estimates of fossil diversity which remains significant even after the removal of the effect of their correlation to geological time, and thus demonstrates the reality of the underlying pattern (Sepkoski *et al.* 1981). Correlation analysis, however, cannot indicate which one of the analysed estimates is the most accurate. Yet they widely differ in many important aspects including the presence or absence of a Palaeozoic plateau in diversity. More importantly the correlation analysis was carried out at the

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system level of stratigraphic resolution and hence cannot substantiate a pattern at the stage level. Finally, a more recent analysis of inherent sampling biases in that data set shows that their quantitative effects may approach an order of magnitude (Signor 1982). Much caution is therefore necessary in any quantitative inference from those data.

Nevertheless, I use Sepkoski's (1982) compilation as a source of data on global family diversity and the rates of family extinction and origination during the Phanerozoic because (i) this is the empirical pattern that diversity curves predicted by the theoretical models were tested against, and (ii) no better set of data on global taxonomic diversity is available. I computed the average family diversity and the probabilistic rates of family origination and extinction for each of the post-Tommotian stratigraphic stages listed in Sepkoski's compilation. Rate of origination was calculated as the number of originations in a stage divided by the number of families extant at the end of the preceding stage. Rate of extinction was computed as the number of extinctions in a stage divided by the number of families that survived from the preceding stage plus all those that originated in the given stage. This procedure assumes that all originations and extinctions were clustered at the beginning and the end of each stage, respectively, but it overcomes the bias of erroneous estimates of the absolute duration of particular stages; analytical error in absolute age determination of stratigraphic boundaries increases significantly with geological age and may exceed stage duration considerably (Odin 1982; Harland *et al.* 1983). Records with stratigraphic resolution at the level of series or system were assigned to the component stages proportionately. Only a negligible minority of the total number of families have stratigraphic ranges shorter than a stage, which attests to appropriateness of the time scale (Mark and Flessa 1977).

Based on this data set, there is a highly significant ($P < 0{\cdot}01$) correlation between family diversity and the rates of family origination ($r = -0{\cdot}594$) and extinction ($r = -0{\cdot}630$) over the seventy-six post-Tommotian stages. This may be artificial, however, for there is a strong correlation between geological time and both taxonomic diversity and taxonomic evolutionary rates at the family level. Family diversity significantly increases (Valentine 1969; Sepkoski *et al.* 1981; Signor 1982), while the rate of family extinction significantly declines through time (Raup and Sepkoski 1982; Van Valen 1984). Spurious correlations may also arise because (i) the analysis involves time series, and (ii) the probabilistic rates of extinction and origination are by definition related to diversity as they contain its measure in the denominator. The data set was therefore subdivided into four time intervals separated by the major extinction events (Ashgillian, Guadelupian-Dzhulfian, Maastrichtian): early Cambrian to late Ordovician, early Silurian to late Permian, early Triassic to late Cretaceous, and early Tertiary to Quaternary. The mass extinctions, however, were not excluded from the analysis because there is no compelling evidence to support their interpretation as outliers (Quinn 1983; Raup *et al.* 1983).

Correlation coefficients between diversity and rates of origination and extinction for each time interval are given in Table 1. Except for the rate of origination in the later Palaeozoic, none of these correlations is significant at $P = 0{\cdot}05$; the correlation of the later Palaeozoic rate of family origination to diversity is nonsignificant at $P = 0{\cdot}02$. Exclusion of the mass extinctions improves the correlations in the later Palaeozoic only. Generally, the correlations do not attain significance over still shorter time intervals. This rules out the possibility that the time scale is too crude to account for changes in the relationship of extinction and origination rates to diversity (Hoffman and Kitchell 1984). Introduction of one-stage time lag between diversity and the rates of origination and extinction does not improve the correlations.

Choice of the level of statistical significance to be regarded as biologically meaningful is always arbitrary, and it might be argued that even $P = 0{\cdot}1$ would not be too liberal a level given the biases inherent in the fossil record. Many correlation coefficients given in Table 1 are significant at that level, but they are all negative which contradicts the concept of converse dependence of the rates of origination and extinction on diversity. The taxonomic evolutionary rates still might converge with increasing diversity. For none of the time intervals, however, is the difference between slopes of the respective regressions significant.

DISCUSSION

This analysis shows the absence of significant correlation between the global taxonomic diversity and taxonomic evolutionary rates. It is crucial to emphasize that the null hypothesis tested in this study predicted the occurrence of such a correlation. The fact that spurious correlations might be expected to arise in the analysed system makes the evidence for rejection of the null hypothesis even more compelling.

It might be argued that the absence of significant correlations is due to the lumping of what Sepkoski (1981; see also Sepkoski and Sheehan 1983) recognized as three consecutive evolutionary faunas into a single biotic system in the present analysis. If two or more distinct groups of taxa, which partly overlap in time, each exhibit their own diversity-dependent extinction and origination rates, there may be no correlation between the total taxonomic evolutionary rates and total diversity as computed for the global biota. The validity of Sepkoski's (1981) factor analytic description of the fossil record is questionable, however, because there is no evidence to support the claim that the evolutionary faunas are anything more than abstract statistical constructs (Hoffman, in press; see also discussion on the reification of factor analytic solutions by Gould 1981). Even if the lack of correlations were the result of lumping Sepkoski's (1981) faunas, this could account for the absence of diversity dependence from the Cambrian to Ordovician only, which indeed covers two distinct faunas. The Silurian to Permian interval, however, covers essentially the Palaeozoic fauna of Sepkoski (1981), with the modern fauna largely congruent in pattern and the Cambrian fauna negligible; the Mesozoic and Cenozoic time intervals, in turn, cover almost exclusively the modern fauna of Sepkoski (1981). Thus, there is no evidence for diversity dependence in the evolutionary behaviour of the alleged faunas either. This result contradicts the assumption that diversity dependence of the rates of family origination and extinction leads to a global equilibrium in diversity. It refutes the macroevolutionary models of biotic diversification based on the logistic equation.

This conclusion does not necessarily imply that the taxonomic diversity of the biosphere increases indefinitely, nor even that its upper limits are set entirely by abiotic resources. First, the data analysed here may be too biased to allow a reliable inference. Secondly, the level of taxonomic resolution may be inadequate if (i) the family is merely a taxonomic artifact with its biological meaning widely variable among organic groups, or (ii) the family/species relationship is widely variable through geological time (due merely to the taxonomic structure we impose on the biota or to the very nature of the evolutionary process; Raup 1983; Flessa and Jablonski, in press). In this case family diversity is meaningless as a measure of biosphere proximity to the limits to specialization and decrease in the average population size and there may be no congruence between the patterns at the family and the species levels. Thirdly, regardless of the existence or not of biotic limits to global diversity, the actual diversity may be primarily controlled by abiotic (Valentine 1973) or biogeographical (Valentine *et al.* 1978; Schopf 1979*b*; Wise and Schopf 1981) factors. Fourthly, the concept of the biosphere responding predictably (even though under a weak, statistical definition of determinism) to perturbations may be wrong, for taxa may not be validly considered as indistinguishable particles (Hoffman 1981, 1983). Identical perturbations may prompt widely variable biotic responses

TABLE 1. Correlation coefficients between taxonomic evolutionary rates and diversity.

Time interval	Number of stages	Rate	Correlation to diversity r
Atdabanian to Ashgillian	14	origination	−0·365*
		extinction	−0·304*
Llandoverian to Dzhulfian	21	origination	−0·458
		extinction	−0·351*
Induan to Maastrichtian	29	origination	−0·322*
		extinction	−0·097*
Danian to Pleistocene	12	origination	−0·512*
		extinction	−0·359*

* Asterisks denote correlations not significant at $P = 0{\cdot}05$.

depending on particular configurations of the biosphere (taxonomic composition, biogeographical structure, etc.). The rates of origination and extinction of taxa may depend primarily on historical contingencies rather than on general laws. The last possibility might account for the observed lack of order but also for the absence of strict randomness (Flessa and Levinton 1975) in the evolution of biotic diversity.

The hypothesis of global equilibrium in species number as the upper limit to the process of biotic diversification is thus compatible with, though not supported by, the empirical data on family diversity, extinction, and origination. They contradict, however, the alleged evidence for its correctness, derived from the apparent fit of the curves predicted by macroevolutionary models of diversification to the empirical pattern. There is no other conclusive evidence to support this hypothesis.

The present results are irrelevant to the hypothesis of regional or continental evolutionary equilibrium as derived from the theory of island biogeography (Rosenzweig 1975; cf. Hoffman, in press). The latter concerns the species level of the taxonomic hierarchy and a much finer time scale.

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A PROTOROTHYRIDID CAPTORHINOMORPH (REPTILIA) FROM THE UPPER CARBONIFEROUS OF NEWSHAM, NORTHUMBERLAND

by M. J. BOYD

ABSTRACT. A description is presented of the skull table of a protorothyridid captorhinomorph reptile from the lower Westphalian B (Upper Carboniferous) of Newsham, Northumberland. The specimen, which is not named, represents the first reptile to be recorded from the Carboniferous of the British Isles and from the north-west European paralic Coal Measures. It is closely contemporaneous with the earliest undisputed reptiles to have previously been described, from the lower Westphalian B of Joggins, Nova Scotia, and is the oldest fossil reptile yet reported from anywhere outside North America.

The specimen forms part of a large assemblage of (mostly aquatic) vertebrates preserved in the bottom sediments of a large coal-swamp lake, and is presumed to represent an erratic derived from a terrestrial/marginal environment.

THE captorhinomorph reptile family Protorothyrididae includes the earliest and most primitive reptiles currently known. The family is represented in the Lower Permian of North America by two named species of *Protorothyris* and by at least two further, un-named, protorothyridid species (Clark and Carroll 1973; Reisz 1980). However, seven genera of protorothyridids, all but one of them monotypic, have so far been described and named from the Upper Carboniferous of Europe and North America. Of the seven genera, five are Westphalian D in age. These comprise *Brouffia* and *Coelostegus* from Nýřany in Czechoslovakia (Carroll and Baird 1972), *Palaeothyris* from Florence, Nova Scotia (Carroll 1969), *Anthracodromeus* from Linton, Ohio (e.g. Carroll and Baird 1972), and *Cephalerpeton*, which is known from both Mazon Creek, Illinois (e.g. Carroll and Baird 1972) and Linton (Reisz and Baird 1983), although apparently represented by a different species at each site. The two remaining described protorothyridid genera, *Hylonomus* and *Archerpeton*, are both from the lower Westphalian B of Joggins, Nova Scotia (Carroll 1964). They, together with the pelycosaur *Protoclepsydrops*, which occurs in the same deposits, constitute the earliest undisputed reptiles known. Although Baird and Carroll (1967) have described *Romeriscus periallus* from the Westphalian A of Cape Breton Island, Nova Scotia, as a limnoscelid reptile, both the limnoscelid status of *Romeriscus* and the reptilian status of limnoscelids are open to doubt (Panchen 1972; Heaton 1980).

In the present paper, an account is given of a hitherto undescribed Upper Carboniferous protorothyridid specimen, the existence of which (as a 'romeriid') was briefly noted by Boyd (1984, p. 392). The specimen does not appear to be referable to any previously described protorothyridid species, but it is too incomplete for any satisfactory diagnosis. It is not, therefore, named. However, Carboniferous protorothyridid fossils are of rare occurrence, and the specimen under discussion merits description by reason of its stratigraphic and palaeobiogeographical importance.

MATERIALS AND METHODS

The specimen, which is registered in the collections of the Hancock Museum, Newcastle upon Tyne, as G24.84, consists of an incomplete skull table. It was collected at some time between 1860 and 1880 by the accomplished amateur palaeontologist Thomas Atthey, and is from the black shale immediately overlying the Northumberland Low Main Seam at Hannah Pit, Newsham Colliery, near Blyth in Northumberland. This horizon lies within the upper *Modiolaris* zone of the Middle Coal Measures (Land 1974) and is thus lower Westphalian B in age.

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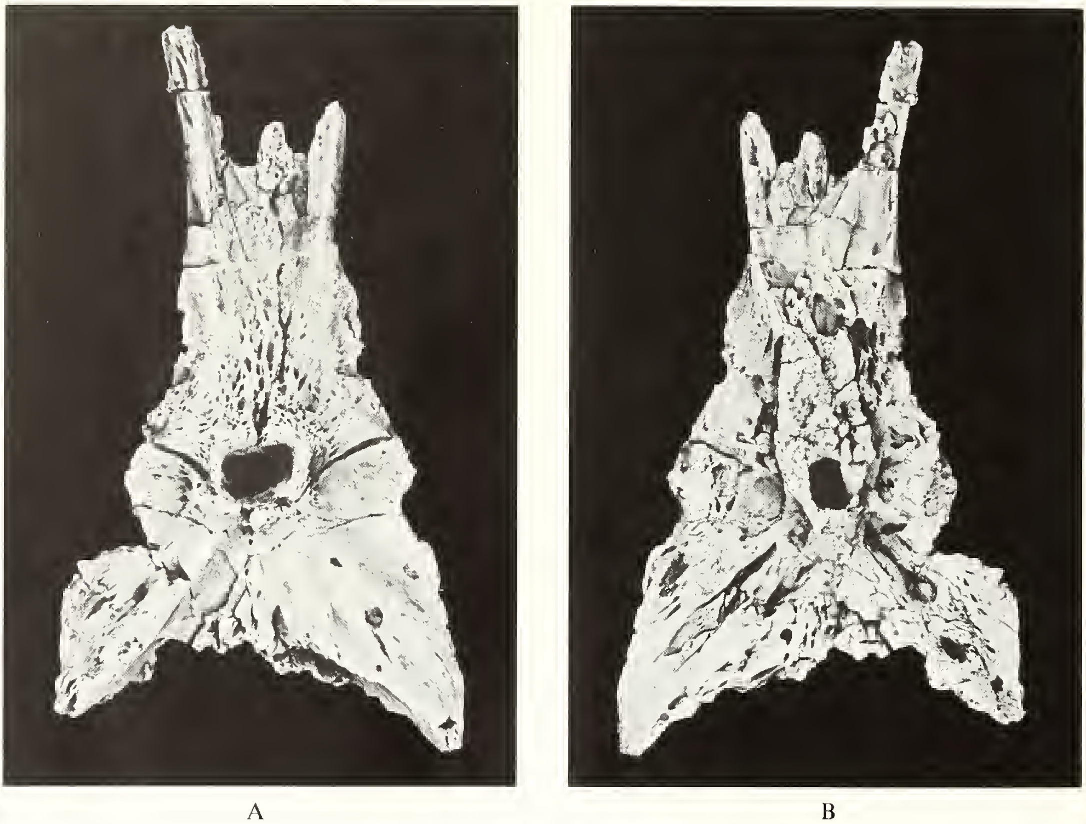

TEXT-FIG. 1. Skull table of protorothyridid reptile, Hancock Museum specimen G24.84, as preserved. A, dorsal view. B, ventral view. Both ×2·5.

The skull table, originally preserved on a small slab of shale, has been completely cleared of matrix by the use of mounted needles and of an S.S. White Industrial Airbrasive Unit (Stucker 1961), employing sodium bicarbonate as the abrasive powder. After preparation the specimen was strengthened by a coat of 'Perspex' applied as a dilute solution in ethyl acetate.

DESCRIPTION

As preserved, specimen G24.84 (text-figs. 1A–B, 2A) consists only of the paired frontal and parietal elements of the skull table. The frontals are truncated anteriorly by a fracture and their original extent in this direction can no longer be determined. The posterolateral 'corners' of both frontals are also absent, as is much of the anterior part of the lateral margin of the left parietal. The left parietal, which

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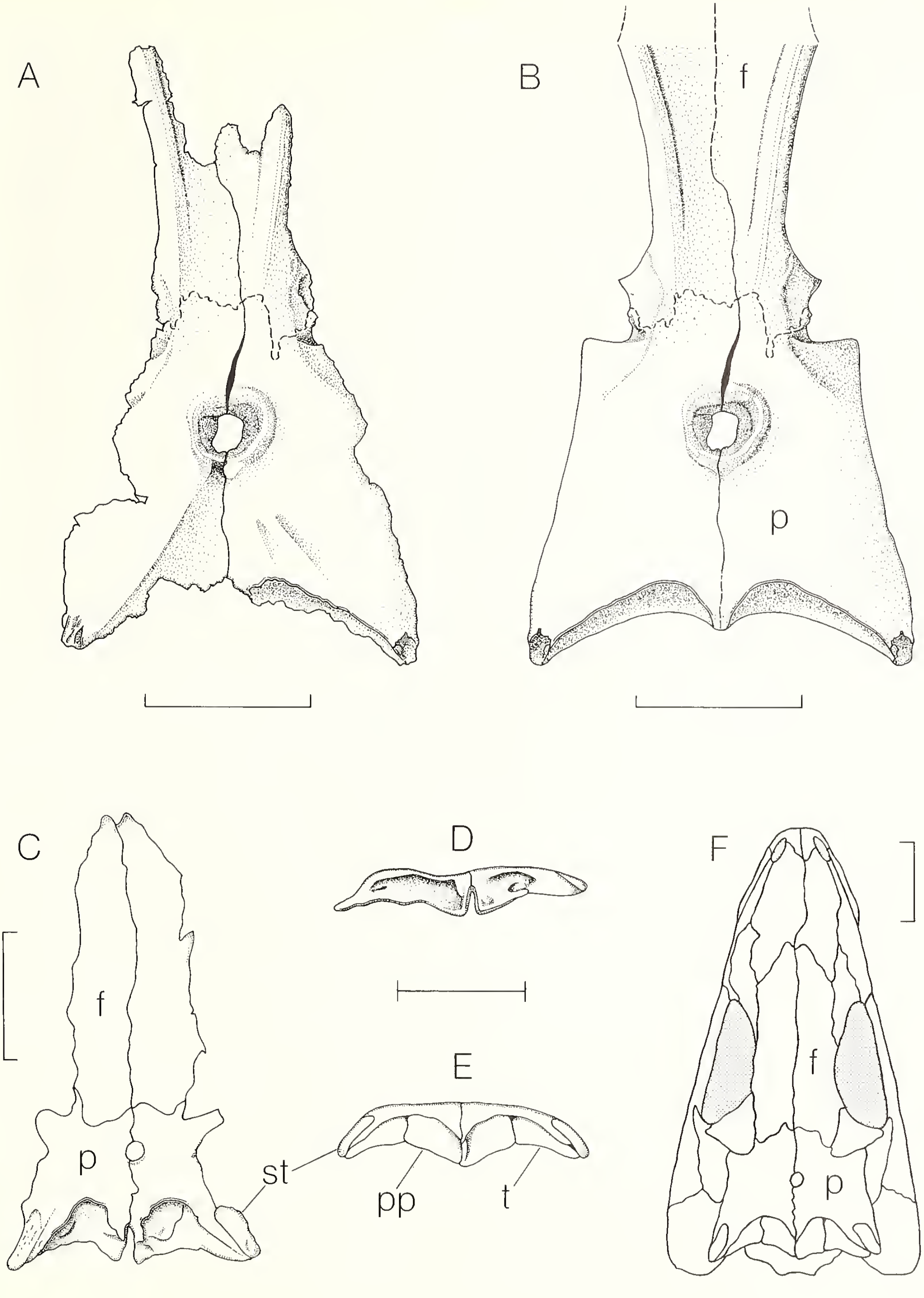
TEXT-FIG. 2. Protorothyridid reptile skulls. A–B, Hancock Museum specimen G24.84 in dorsal view: A, as preserved. Ornament and cracks omitted for sake of clarity; B, suggested restoration. Ornament omitted. C–F, *Protorothyris archeri*: C, holotype skull table in dorsal view, as preserved. Cracks and ornament omitted; D, holotype skull table in posterior view, as preserved; E, skull table in posterior view, restored; F, skull in dorsal view, restored (C–F modified from Clark and Carroll 1973, figs. 2–3). All scale bars represent one centimetre. Abbreviations: f—frontal; p—parietal; st—supratemporal; pp—postparietal; t—tabular.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also lacks most of its posterior edge, has suffered severe distortion during preservation, resulting in a mesial shift in position of the parietal 'horn'. That it is the left, and not the right, parietal which is distorted is confirmed by the contrast between the 'crazed' ventral surface of the former and the smooth, well-preserved ventral surface of the latter (text-fig. 1B). A large crack crosses the specimen at the level of the parapineal foramen and many smaller cracks are present. The mid-line suture of the skull-table is, none the less, clearly distinguishable in both dorsal and ventral views. That passing transversely between the frontals and parietals is, however, apparent in its entirety only in ventral view. The course of the latter suture is, therefore, depicted as a broken line in the illustrations of the skull table in dorsal view (text-fig. 2A–B), since dermal skull roofing bones often have sloping suture faces which are not perpendicular to their outer surfaces (Milner 1978, p. 673). In G24.84 the parietals appear slightly to overlap the dorsal surfaces of the frontals.

The lateral margins of both frontals are thickened for most of their preserved lengths, suggesting a rather more extensive orbital exposure than is the case in any of the described Westphalian D protorothyridids (Carroll and Baird 1972). However, the frontals of *Hylonomus*, which is closely contemporaneous with G24.84, also enter more largely into the mesial margins of the orbits than those of later protorothyridids, having orbital exposures for approximately half their total lengths (Carroll 1964, fig. 2). In G24.84 as preserved, the thickened lateral rims of the frontals are more apparent dorsally than ventrally; it is possible, however, that this is an artefact produced by downward crushing of the thinner mesial part of each element during preservation. The frontals bear little ornament except posteriorly, where they exhibit shallow elongate pits mesially and a much more subdued ornament of tiny pits near their lateral edges (text-fig. 1A).

Any description of the parietals must of necessity be based largely upon the right element. This is a large bone, thickening towards its posterior margin and drawn out posterolaterally into a tapering 'horn'. The lateral margin of the right parietal is well-preserved in its posterior half. The bone becomes progressively thinner as the margin is approached and this fact, together with the simple contour presented by the line of the edge itself, would seem to indicate the absence (in the complete skull) of any skull table elements lateral to the parietals in this region. As in all described protorothyridids, the parietals of G24.84 appear to have formed the posterior edge of the horizontal dorsal surface of the skull, the postparietals, tabulars, and supratemporals having been relegated in part to the upper occipital region. The right parietal is embayed posteriorly, bearing a shallow transverse depression in the dorsal part of its posterior edge, below which a thin shelf of bone (damaged in the specimen) extends backwards. The surface of the depression and the dorsal surface of the shelf are slightly roughened. A similar situation exists in all protorothyridids in which this region of the skull has been described, where the posterior recesses in the parietals (text-fig. 2C–D) house the postparietals and tabulars (text-fig. 2E–F). Both parietals of G24.84 exhibit a shallow notch in the dorsal surface of the tip of the parietal 'horn'. Similar notches are present in this position in the known protorothyridids and serve to receive the anterior extremities of the supratemporal bones. The parapineal foramen is large and is surrounded dorsally by a slightly raised rim. Ventrally the foramen is also surrounded by a raised area of bone; this, however, extends forward to the level of the fronto-parietal sutures and presumably represents an area of contact between neurocranium and dermal skull roof. The ornament of the parietals is largely restricted to the region anterior to the parapineal foramen, where deep anteroposteriorly elongate pits, becoming shallower and less elongate laterally, are present (text-fig. 1A). The nature and distribution of the parietal ornament, and that of the frontal elements, appear to be typical of Carboniferous protorothyridids (e.g. Carroll 1969; Carroll and Baird 1972).

DISCUSSION

Despite the very incomplete nature of specimen G24.84 there can be little doubt that it pertains to a protorothyridid reptile. It cannot be referred to any known group of Palaeozoic fish (see e.g. Moy-Thomas and Miles 1971). In addition, the following features of the specimen together preclude reference to any known group of Palaeozoic Amphibia and indicate its reptilian status:

1. The absence of any dermal bones in the skull table lateral to (at least the posterior halves of) the parietals.
2. The formation of the posterior edge of the horizontal skull table by the parietals.
3. The embayment and recessing of the posterior margins of the parietals (presumably for the reception of the postparietals and tabulars).
4. The dorsal notches on the tips of the parietal 'horns' (presumably for the reception of the anterior extremities of the supratemporals).

Although the oldest known species of synapsid reptile, *Protoclepsydrops haplous* Carroll, 1964, occurs at Joggins and demonstrates that the Pelycosauria were in existence by (at least) lower Westphalian B times, it does not seem that G24.84 can be regarded as pertaining to a pelycosaur. Non-pelycosaurian features of G24.84, which are, however, compatible with protorothyridid status, include:

1. The form of the frontal elements. The frontal elements are not known for *Protoclepsydrops* but those of the oldest known pelycosaur in which these bones have been described, *Archaeothyris* from the Westphalian D of Linton, Nýřany and Florence, Nova Scotia (Reisz 1972; 1975), differ in at least three ways from those of G24.84. They are, relatively, somewhat wider structures, and they have much more restricted exposures in the orbital margins. Most importantly, that part of each frontal which is exposed in the rim of the orbit is a distinct lateral process of the element (Reisz 1972; Kemp 1980, fig. 1b). The presence of this lateral process is the usual pelycosaurian condition (Langston and Reisz 1981, p. 76), although absent in the family Varanopidae. Varanopids, however, are known only from the Permian. The frontals of G24.84 lack any lateral processes of pelycosaurian type.
2. The proportions of the parietals. Those of both *Protoclepsydrops* (Carroll 1964, fig. 13A) and *Archaeothyris* (Reisz 1972; Kemp 1980) appear to be significantly wider relative to their length than those of G24.84.

Excepting the extent to which the frontals enter into the orbital margins, there do not seem to be any structural features of G24.84 which would positively preclude its being the skull table of a captorhinid, rather than a protorothyridid, reptile. However, the proportions of the specimen are certainly more suggestive of the high, narrow skulls characteristic of protorothyridids than of the lower and wider skulls which characterize known captorhinids (Reisz 1980). Moreover, G24.84 is considerably older than the earliest known captorhinids (Heaton 1979), which are thought to have evolved from protorothyridid ancestors (Clark and Carroll 1973).

The tentative restoration of specimen G24.84 (text-fig. 2B) is based upon the assumption of bilateral symmetry. It has also been assumed that the complete frontals were, like those of *Hylonomus*, approximately the same length as the parietals, and that the posterior recessing of the parietals, to accommodate the postparietals and tabulars, was (as in other Carboniferous protorothyridids) rather less extensive than in *Protorothyris* itself. The asymmetry of the ventral opening of the parapineal foramen and the dorsal depression between the thickened lateral margins of the frontals have been retained in the attempt at reconstruction, it being uncertain whether or not these two features are artefacts resulting from *post-mortem* distortion of the specimen.

Specimen G24.84 represents the first reptile to be recorded from the Carboniferous of the British Isles and from the north-west European paralic Coal Measures as a whole. It is also the oldest fossil reptile yet described from anywhere outside North America, and is closely contemporaneous with the earliest undisputed reptiles previously described (the protorothyridids *Hylonomus* and *Archerpeton* and the pelycosaur *Protoclepsydrops* from Joggins).

The Newsham protorothyridid specimen forms part of a large and diverse assemblage of tetrapods from the site. In a recent palaeoecological review (Boyd 1984), the present writer divided the (then) eight known Newsham tetrapod species, which were certainly determinate at least to family level, into three ecological associations, derived from different environments. The criteria employed were the relative frequency of the various taxa present, the size distribution and degree of articulation of the specimens, the functional morphology of the animals themselves, and the environmental and faunal contexts in which the taxa present occurred elsewhere. The environment of preservation of the Newsham tetrapods appears to have been a large and deep freshwater lake, occupying a stretch of abandoned river channel in which peat had previously accumulated (Boyd 1984), and there can be little doubt that G24.84 represents an erratic from a terrestrial/marginal tetrapod community, probably (judging by the nature of the specimen) transported into the lake *post-mortem*. It is the only protorothyridid specimen recorded from the site and although, as pointed out by Romer (1974), the known Carboniferous protorothyridids were probably 'persistent coal-swamp dwellers', they show no evidence of aquatic adaptation. On the contrary, their well-developed limbs and well-ossified skeletons suggest that (by coal-swamp standards at least) they were active terrestrial animals (Carroll 1969; Carroll and Baird 1972). The essentially terrestrial nature of Carboniferous protorothyridids is also indicated by the fact that, of the five large, compact Westphalian tetrapod assemblages currently known (those from Jarrow in Co. Kilkenny (Ireland), Newsham, Joggins, Nýřany, and Linton), only that from Joggins includes members of this family as other than very rare components. Whereas the tetrapods at the other four sites are preserved in sediments deposited in bodies of standing water (e.g. Rayner 1971; Boyd 1984; Milner 1980), those from Joggins are preserved in sediments laid down originally in the upright, hollow stumps of large lycopods, which functioned as pit-fall traps for small terrestrial animals (Carroll 1967). Significantly, protorothyridids, very rare at Nýřany (Milner 1980), Linton (Reisz and Baird 1983), and Newsham and not reported from Jarrow, are represented at Joggins by at least eighteen specimens of *Hylonomus* and sixteen of *Archerpeton* (Carroll *et al.* 1972).

The description of protorothyridid specimen G24.84 increases the number of tetrapod species (certainly determinate at least to family level) whose presence at Newsham has been established, from the eight listed by Boyd (1984, p. 372) to nine. An updated 'faunal' list of the tetrapods so far reported from the site is given below, with the taxa present grouped into the three ecological associations represented in the assemblage:

1. *Terrestrial/marginal association*. Two species—the anthracosaurid embolomere *Anthracosaurus russelli* Huxley and an un-named protorothyridid captorhinomorph reptile.
2. *Shallow-water/swamp-lake association*. Four species—the ophiderpetontid aïstopod *Ophiderpeton nanum* Hancock and Atthey, a urocordylid nectridean, a lysorophid (the latter two not determinate below family level) and, less certainly, the eogyrinid embolomere *Pteroplax cornutus* Hancock and Atthey.
3. *Open-water/lacustrine association*. Three species—the loxommatid *Megalocephalus pachycephalus* Barkas, the keraterpetontid nectridean *Batrachiderpeton reticulatum* (Hancock and Atthey), and the eogyrinid embolomere *Eogyrinus attheyi* Watson.

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LOWER ORDOVICIAN TRILOBITES FROM THE HANADIR SHALE OF SAUDI ARABIA

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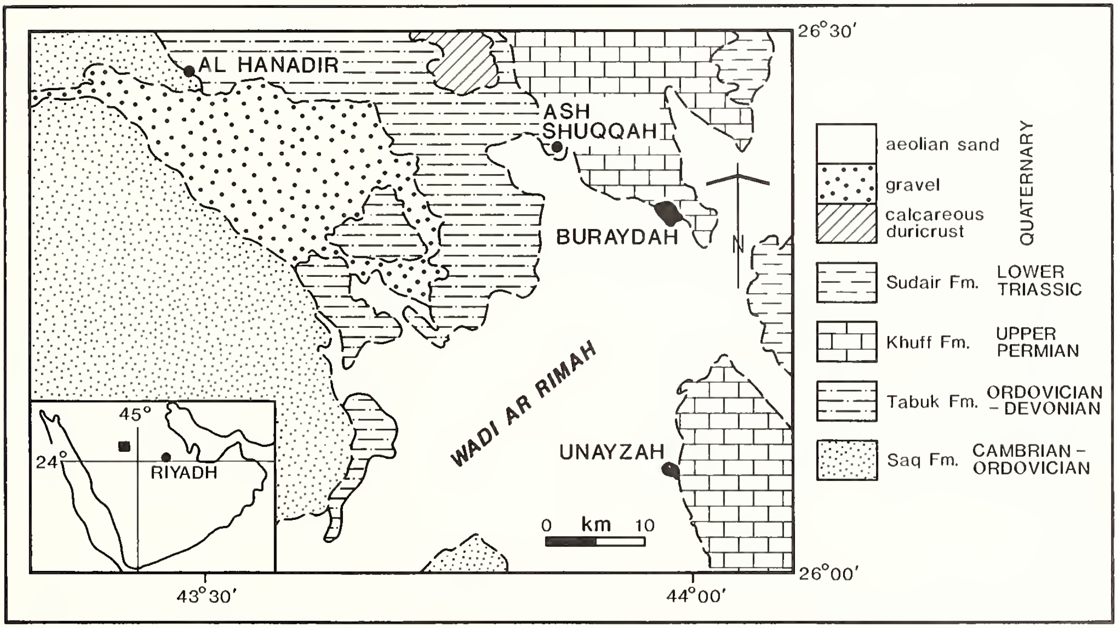
ABSTRACT: Recent collections from the Hanadir Shale (Llanvirn) include a more diverse trilobite fauna than was originally known. In addition to the previously described *Plaesiaconia vacuvertis* and *Neseuretus* (*Neseuretus*) *tristani* the following have been recognized: *N.* (*N.*) cf. *tristani*, *P.* sp. aff. *P. rara*, *Kerfornella* sp., *Kloucekia* sp., *Ningkianolithus hanadirensis* sp. nov., and asaphid indet. The fauna also includes graptolites, brachiopods, bivalves, ostracods, and orthocones. The trilobites confirm the 'Gondwanan' aspect of the fauna.

THIS paper presents a record of Lower Ordovician trilobites from the Hanadir Shale (Member) of the Tabuk Formation, Saudi Arabia. The trilobites were collected by one of us (A.A. El-K.) at Al Hanadir (26° 27′ 50″ N., 43° 27′ 20″ E.) about 53 km west-north-west of Buraydah, Al Qasim Province (text-fig. 1). Thomas (1977) had earlier described and figured *Plaesiaconia vacuvertis* Thomas from the type locality (erroneously quoted by Thomas as 25° 28′ 00″ N.) and recently Fortey and Morris (1982) figured *Neseuretus* (*Neseuretus*) *tristani* (Desmarest, 1817) from the Hanadir Shale further north. No other trilobites have been recorded or figured from this unit and so the recently discovered material is of interest.


26°30′
AL HANADIR
ASH SHUQQAH
BURAYDAH
N
WADI AR RIMAH
UNAYZAH
0 km 10
26°00′
43°30′
44°00′
45°
24°
RIYADH
aeolian sand
gravel
calcareous duricrust
QUATERNARY
Sudair Fm. LOWER TRIASSIC
Khuff Fm. UPPER PERMIAN
Tabuk Fm. ORDOVICIAN – DEVONIAN
Saq Fm. CAMBRIAN – ORDOVICIAN

TEXT-FIG. 1. Geological map of Al Qasim Province, Saudi Arabia, showing location of Al Hanadir section (see text-fig. 2). From Bramkamp *et al.* 1963.

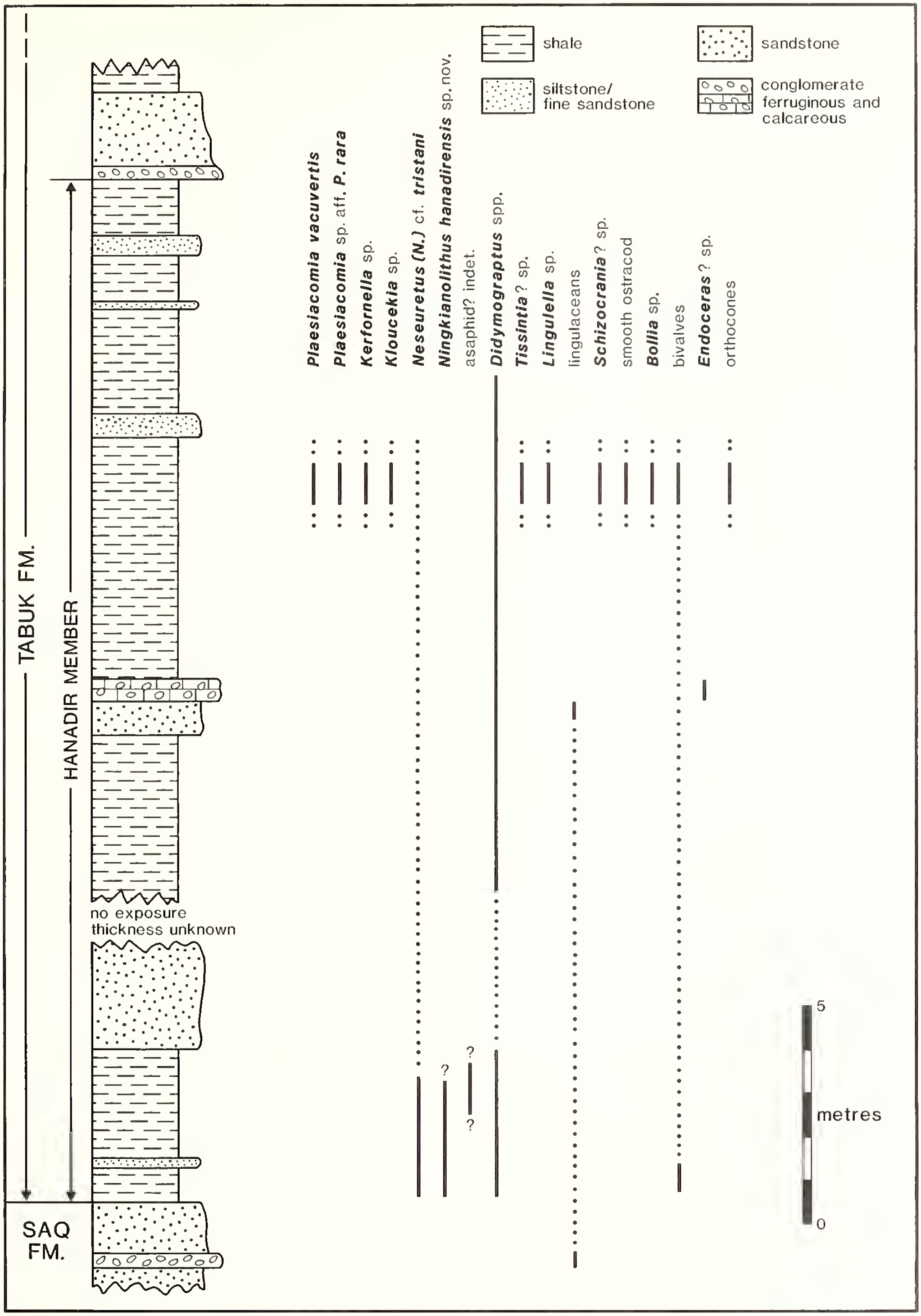
[Palaeontology, Vol. 28, Part 2, 1985, pp. 401–412, pl. 47.]

The lithostratigraphy of the Tabuk Formation has been described by Thralls and Hasson (1956), Steineke *et al.* (1958), Helal (1964, 1968), Powers *et al.* (1966), and McClure (1978). According to Powers *et al.* (1966) the Tabuk Formation (lower Ordovician to lower Devonian) rests conformably but with a sharp contact on the sandstones of the Saq Formation which is of possible Cambrian to lower Ordovician age. Helal (1964), however, regarded the contact as being disconformable. We prefer to follow Powers *et al.* (1966), although it is recognized that at present there is no strong faunal evidence. The top few metres of the Saq Formation consist of medium-grained, cross-bedded, sandstones with ripple marks up to 20 cm in wavelength. Approximately 1·5 m below the base of the Hanadir Member (text-fig. 2) is a thin (20 cm) conglomerate with sandstone pebbles up to 30 cm across and containing disarticulated and broken valves of lingulacean brachiopods in the matrix. This bed is overlain by fine-grained sandstones with *Cruziana* and bundles of traces resembling *Arthrophycus*. The presence of *C.* cf. *furcifera*, *C. luberi* (see Powers *et al.* 1966) and *C. goldfussi* (see Helal 1968) suggests a possible Arenig age for this part of the unit. The association of lithofacies and trace fossils resembles the lower Ordovician pebbly channel-sand facies of Jordan, described by Selley (1970). Beds containing lingulacean debris are found at a similar horizon in central Portugal and Brittany where they occur at the top of the Armorican Quartzite. The Hanadir Shale forms the basal member of the Tabuk Formation and varies in thickness from 12·2 to 68·5 m (Powers *et al.* 1966, pp. D112–113). At Al Hanadir it is at least 23 m thick; this is based on the 2 m thick sandstone bed shown in text-figure 2 as representing the base of the overlying sandstone unit (unit 2 of Powers *et al.* 1966). There is a gap in the exposure, however, in the lower part of the sequence. The Hanadir Member consists mainly of pale buff to greenish-brown shale, occasionally gypsiferous and limonitic, with thin beds of siltstone, fine sandstone, and ferruginous, calcareous conglomerate. The 2 m thick sandstone bed overlying the Hanadir Member has a conglomeratic base with abundant brachiopod debris dominated by lingulaceans.

Graptolites from the Hanadir Shale have been known since 1947 (see Powers *et al.* 1966, p. D25) and were later identified by R. J. Ross, Jr. as *Didymograptus protobifidus* Elles. McClure (1978) regarded the graptolites from the shale as indicating an upper Llanvirn, *murchisoni* Biozone age and stated (p. 324) that '. . . Trilobites and a rich chitinozoan and acritarch assemblage substantiated this age assignment'. On the basis of previous graptolite determinations, Dean (1980, p. 8 and table) considered the Hanadir Shale to range in age from upper Arenig to top Llanvirn. Khashogji (1979) concluded that the *murchisoni* Biozone was indicated for assemblages occurring 1·5–2·0 m above the base. The most recent reference to the graptolite fauna was by Fortey and Morris (1982, p. 68) who listed *D. murchisoni*, *D.* cf. *geminus*, *D. artus*, and *D.* cf. *spinulosus* and concluded that an upper Llanvirn age is likely. Fortey and Morris figured *N.* (*N.*) *tristani* from within the graptolitic sequence and recorded associated inarticulate brachiopods (*Schizocrania*?, *Monobolina*, *Lingulella*) as well as the bivalve *Glyptarca* cf. *narajoana* (Verneuil and Barrande).The assemblage from the Hanadir Shale indicates that the unit contains a more diverse trilobite fauna than was originally thought and provides additional information on the affinities and provincialism of the fauna.

AGE OF THE TRILOBITE FAUNAS

In the shales immediately overlying the sandstones of the Saq Formation there occurs a restricted assemblage of trilobites (*Ningkianolithus hanadirensis* sp. nov., *Neseuretus* (*Neseuretus*) cf. *tristani*, and an indeterminate asaphid) associated with rare pendent graptolite fragments and bivalves. *Ningkianolithus* occurs in the Shirgesht Formation of Iran, where it is associated with other trilobites indicating 'both Lower and Middle Ordovician horizons' (Dean 1980, p. 18; Ruttner *et al.* 1968, pp. 35–36). In China, where it occurs with abundant *Neseuretus* (Lu 1975; Sheng 1980, table 4), *Ningkianolithus* is known from the Dawan and Meitan Formations of upper Arenig age. *Neseuretus* (*N.*) *tristani* is not recorded from beds of Arenig age and Fortey and Morris (1982) regarded the species as being a typical Llanvirn form which 'extended over much of Gondwanaland'. Hammann (1983, p. 57), however, considered the species to be of Llandeilo age in Spain, the subspecies *tristani tristani* being restricted to the lower Llandeilo. The older Iberian species, *N.* (*N.*) *leonensis* and


TABUK FM.
HANADIR MEMBER
SAQ FM.
no exposure
thickness unknown
shale
sandstone
siltstone/
fine sandstone
conglomerate
ferruginous and
calcareous
Plaesiacomia vacuvertis
Plaesiacomia sp. aff. *P. rara*
Kerfornella sp.
Kloucekia sp.
Neseuretus (N.) cf. *tristani*
Ningkianolithus hanadirensis sp. nov.
asaphid? indet.
Didymograptus spp.
Tissintia ? sp.
Lingulella sp.
lingulaceans
Schizocrania ? sp.
smooth ostracod
Bollia sp.
bivalves
Endoceras ? sp.
orthocones
?
?
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5
metres
0

TEXT-FIG. 2. Simplified geological section through the Hanadir Member at Al Hanadir (26° 27′ 50″ N., 43° 27′ 20″ E.).

N. (*N.*) *avus* are of Arenig to ?lower Llanvirn, and Llanvirn age respectively (Hammann 1983, pp. 58-63). Thus the age of the *Ningkianolithus-Neseuretus* (*Neseuretus*) association in Saudi Arabia remains unproven for the present. Although the genus *Ningkianolithus* is apparently restricted to rocks of Arenig age the presence of *Neseuretus* (*N.*) cf. *tristani*, together with the indeterminate pendent graptolites, suggests that the assemblage is younger. We consider a lower Llanvirn age to be most likely for the lowest beds of the Hanadir Shale.

A more diverse assemblage (with five trilobite species, brachiopods, bivalves, graptolites, and ostracods) occurs a further 10 m or so higher up the sequence (text-fig. 2). A gap in the section near the base of the Hanadir Shale precludes a more accurate determination of the vertical separation. This assemblage is of upper Llanvirn age as deduced from the graptolites (see earlier); the trilobites are as yet inconclusive. *N.* (*N.*) *tristani* ranges in age from Llanvirn to Llandeilo elsewhere (see above); *Plaesiacomia vacuvertis* is known only from the Hanadir Shale while *P. rara* is of Caradoc age in Bohemia and *P.* cf. *rara* and *P.* n. sp. aff. *rara* (Henry 1980) are of Llandeilo and Caradoc age respectively in north-western France. *Kerfornella* has been recorded from the Llanvirn at Crozon and Normandy (Henry 1976, 1980) and the present record extends the known geographical range of the genus. The incomplete specimens of *Kloucekia* sp. do not allow any close comparisons to be made. Also at this level are inarticulate brachiopods and *Tissintia*? sp. (the latter being few and fragmentary) and at least two species of ostracods, one being a smooth and elongate form, the other provisionally referred to *Bollia*.

AFFINITIES OF THE TRILOBITE FAUNAS

In the light of the recent paper by Fortey and Morris (1982) some comments may be made on the distribution and significance of the faunas. The Saudi Arabian assemblages contain elements known from widely separated areas within 'Gondwanaland' as understood by Cocks and Fortey (1982) and Fortey and Morris (1982). For example, *Ningkianolithus* and *Neseuretus* are common in the lower Ordovician of China while *Plaesiacomia*, *Kerfornella*, *Kloucekia*, and *Neseuretus* are typical genera of this age in western Europe and North Africa. Thus the Arabian faunas show mixing of east and west elements and indicate the general uniformity of conditions and an absence of any major barrier to dispersion along the shallow, shelf seas of that palaeocontinent. We are, therefore, in agreement with Fortey and Morris that southern Europe was not separated from North Africa by a 'Proto-Tethys' (Whittington and Hughes 1972) ocean during the Lower Ordovician.

THE ASSOCIATION OF *NESEURETUS* AND *PLAESIACOMIA*

Fortey and Morris regarded the association of *Neseuretus* with the inarticulate brachiopods *Schizocrania*?, *Monobolina*, and *Lingulella*, and bivalve *Glyptarca* cf. *narajoana* as an inshore, low diversity fauna from clastic facies. They also mentioned *Plaesiacomia* as showing a restricted, boreal distribution in the lower Ordovician (Dean 1976) but argued that it is generally found in deeper water facies than *Neseuretus*. The distribution of *Plaesiacomia* during the lower Ordovician parallels that of *Neseuretus*, although showing a more restricted range, and the suggestion that *Plaesiacomia* is a 'deeper water' genus is difficult to substantiate from what is known of assemblages from Iberia and Brittany. *Plaesiacomia* and *Neseuretus* are now known to coexist in the following areas: Brittany and Normandy (Henry 1980); Spain (Hammann and Henry 1978; Hammann *et al.* 1982; Hammann 1983), Portugal (Cooper 1980; Romano 1982; Hammann *et al.* 1982), Morocco (Destombes 1976), and Saudi Arabia. Although Fortey and Morris stated that the *Neseuretus* fauna (*Neseuretus* community type of Fortey and Owens 1978) is characteristic of a clastic facies, the same may be said for *Plaesiacomia* since it too occurs in a range of lithotypes from fine siltstones ('shales') to sandstones. Thus it is difficult to envisage a 'deeper water facies' for *Plaesiacomia* based solely on distribution and associated rock type, and although the present authors would not disagree that the presence of the *Neseuretus* fauna indicates a former inshore facies fringing Gondwanaland, a similar argument may be applied to *Plaesiacomia*. There is as yet no strong evidence to suggest that *Neseuretus* is the shallower water form of the two.

SYSTEMATIC PALAEONTOLOGY

The stratigraphic horizons given below are in most cases measured from the top of the Hanadir Shale, i.e. the base of the 2 m thick sandstone bed mentioned above. This is because at present there is an unknown thickness of shale towards the base of the unit. Specimen number prefixes It and H refer to British Museum (Natural History) and Geology Department, King Saud University, Riyadh, respectively.

Family CALYMENIDAE Burmeister, 1843
Subfamily REEDOCALYMENINAE Hupé, 1955
Genus NESEURETUS Hicks, 1873
Subgenus NESEURETUS (NESEURETUS) Hicks, 1873

Type species. Calymene parvifrons var. *murchisoni* Salter, 1865 (see Whittard 1955, p. 139; Fortey and Morris 1982, p. 69).

Neseuretus (*Neseuretus*) *tristani* (Brongniart *in* Desmarest, 1817)

For synonymy see Henry (1970, 1980), Sadler (1974), Fortey and Morris (1982), and Hammann (1983). Fortey and Morris (1982, p. 70) attributed this species to Desmarest while Hammann (1983, p. 63) attributed it to 'Brongniart *in* Desmarest 1817'.

Neseuretus (*Neseuretus*) cf. *tristani* (Brongniart *in* Desmarest, 1817)

Plate 47, figs. 8–12

Material. Over fifty cephala, cranidia, and pygidia; internal and external moulds.

Horizon. From the base of Hanadir Shale and probably up to at least level of abundant *P. vacuvertis*, about 7 m from the top.

Discussion. As Fortey and Morris stated (1982, p. 72), this species has been revised recently (Henry 1970, 1980; Sadler 1974; and also Hammann 1983) and no further description is necessary. The minor differences noted by Fortey and Morris between the pygidium in their material and that described by Henry is partly substantiated in the present specimens where no more than eight axial rings have been observed but up to seven may be defined across the midpart of the axis. We are in agreement with Fortey and Morris that a specific distinction cannot be made on this character alone. However, despite the close similarity to *N.* (*N.*) *tristani* we only compare our material to that species since all our specimens consistently show more backwardly directed S2 glabellar furrows and never the transversely directed S2 typical of that species (see Henry 1970; Hammann 1983, etc.). Also the frontal border, although long, is not so steeply upturned as in *N.* (*N.*) *tristani.*

Hammann (1983) distinguished two subspecies of *N.* (*N.*) *tristani*: *tristani tristani* and *tristani tardus*. The differences between the two are slight (Hammann 1983, p. 69) and it was not possible to assign the present material to either of the subspecies with any certainty.

Family HOMALONOTIDAE Chapman, 1890
Subfamily KERFORNELLINAE Henry, 1980
Genus KERFORNELLA Henry, 1976

Type species. Asphus brevicaudatus Deslongchamps, 1825.

Kerfornella sp.

Plate 47, fig. 1

Material. H81. Internal mould of pygidium.

Horizon. Unknown but probably at level of *P. vacuvertis*; about 7 m below the top of the Hanadir Shale.

Description. Pygidium nearly twice as wide as long, although posterior margin poorly preserved. Anterior margin strongly and evenly curved. Anteriorly axis nearly half width of pygidium, narrowing evenly backwards to third axial ring, posterior to which there is a slight bulge. Axis delimited by well-marked furrows except at tip. Two anterior ring furrows best defined, except medianly where slightly forwardly flexed. Third furrow weak; fourth furrow barely present, marked by faint distal portions. Terminal piece about one-third length of axis. Pleural lobes with four pairs of furrows not reaching border, fourth pair very faint. Strong articulating furrow on axis continues into well-marked furrows on lobes which are truncated abaxially. Faint vincular furrow(?) present just posterior to pygidial axis. Pygidium gently convex (trans.); longitudinally the axis is most strongly curved posterior to the third axial ring furrow.

Discussion. The semi-circular outline, poorly defined axis posteriorly, and number of axial rings and pleurae agree well with the diagnosis of the genus given by Henry (1976, p. 666). Henry (1980, 1981) illustrated pygidia of four species of *Kerfornella* from north-western France. The specimen from the Hanadir Shale differs from *K. besnevillensis* (Bigot) and *K. morieri* (Bigot) in having fewer axial rings and a less well-defined posterior margin to the axis. *K. miloni* Henry conversely shows weaker axial ring furrows and pleural furrows. *K. brevicaudata* (Deslongchamps) possesses only one axial ring furrow, although Hammann (1983, p. 99) illustrates a pygidium with a weakly developed second furrow. *K. barrandei* (Hammann 1983) does not possess furrows on the pleural lobes and the axial furrows are straighter.

Genus PLAESIACOMIA Hawle and Corda, 1847

Type species. Plaesiacomia rara Hawle and Corda, 1847.

Plaesiacomia vacuvertis Thomas, 1977

Plate 47, figs. 3–5, 7

1977 *Plaesiacomia vacuvertis* sp. nov.; Thomas, pp. 164–168, pl. 23, figs. 6, 8–11; pl. 24, figs. 1–6.

Material. H60–H68 containing at least twenty-three cephala and cranidia, five pygidia and thoracic segments; preserved as internal and external moulds. H82 is an internal mould of an almost complete individual.

Horizon. Most of the specimens are probably from about 7 m below the top of the Hanadir Shale.

Discussion. This species was fully described and figured by Thomas (1977). Little need be added to Thomas's description except to note that in the adults examined in the present material a high proportion showed glabellar furrows, albeit weak; they were not absent as Thomas indicated. Some pygidia possess up to four axial rings which is more than Thomas observed in his material.

Plaesiacomia sp. aff. *Plaesiacomia rara* Hawle and Corda, 1847

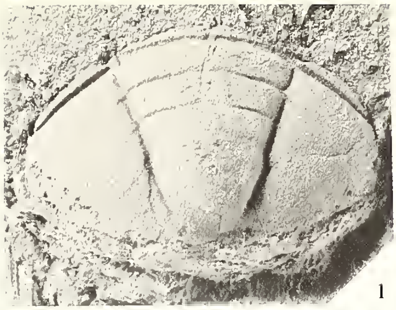
Plate 47, fig. 6

Material. H69/70. Part and counterpart of incomplete cranidium.

Horizon. Unknown but probably at level of *P. vacuvertis*; about 7 m below the top of the Hanadir Shale.

EXPLANATION OF PLATE 47

Fig. 1. *Kerfornella* sp. H81, × 3.
Fig. 2. *Kloucekia* sp. H71, × 3.
Figs. 3–5, 7. *Plaesiacomia vacuvertis* Thomas, 1977. 3, H66, × 4; 4, H68, × 4·5; 5, H62, × 5·5; 7, H64, × 6.
Fig. 6. *Plaesiacomia* sp. aff. *Plaesiacomia rara* Hawle and Corda, 1847. H69, × 6.
Figs. 8–12. *Neseuretus* (*Neseuretus*) cf. *tristani* (Brongniart *in* Desmarest, 1817). 8, H20, × 2; 9, H8, × 5; 10, H54, × 5; 11, H51, × 3; 12, H2, × 4.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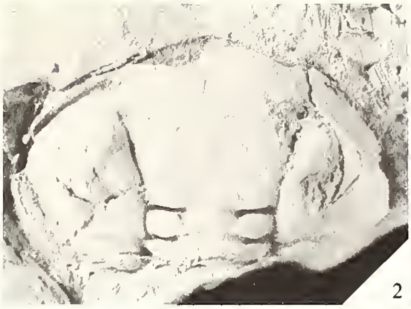
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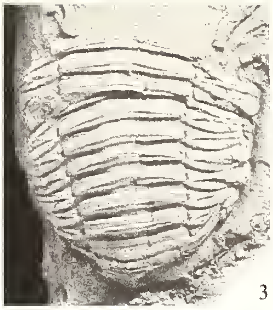
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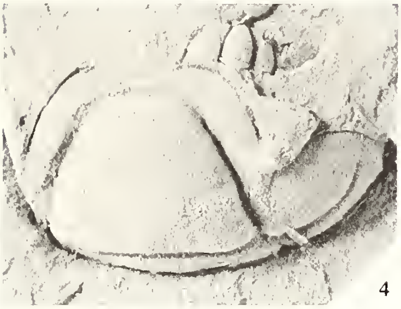
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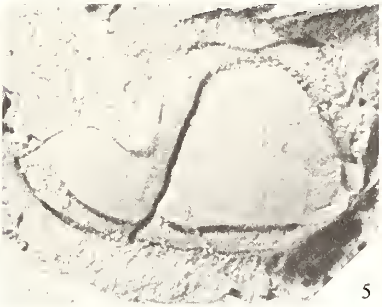
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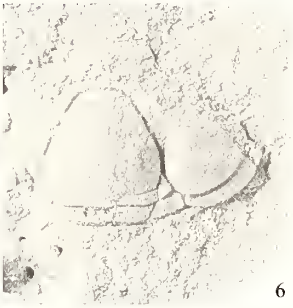
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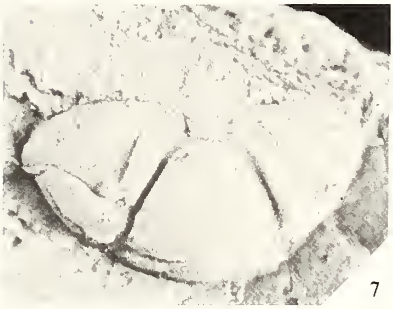
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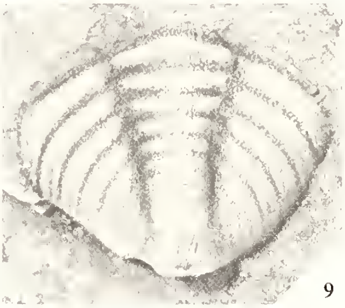
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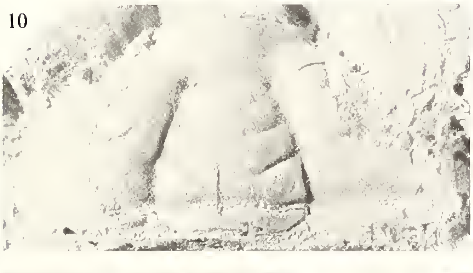

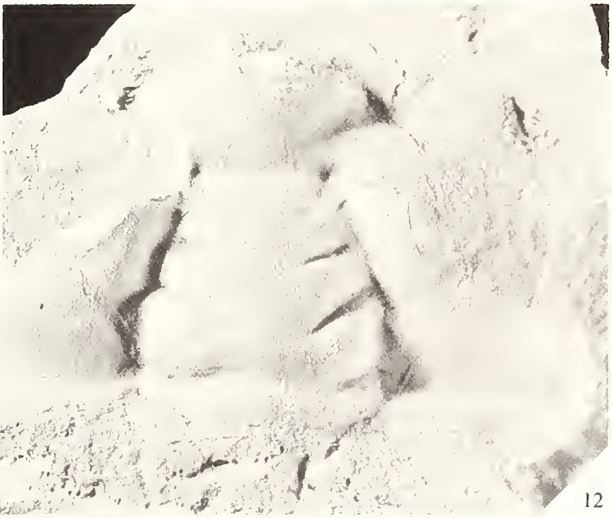
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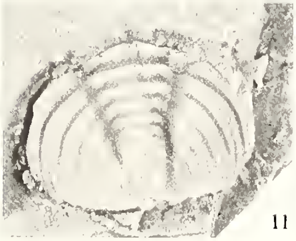
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EL-KHAYAL and ROMANO, *Ordovician trilobites*

Description. Glabella slightly wider than long, anterior width just over one-quarter of posterior width. Glabella sides nearly straight except at posterior end where there is a flexure in axial furrow (paraglabellar area). Axial furrows deepest anterior to paraglabellar areas; along anterior margin of glabella, furrow widens slightly; median part of glabella indented on internal mould. Possible trace of basal glabellar furrows anterior to paraglabellar areas. Frontal area narrow, increasing slightly in width abaxially. Occipital ring of uniform width, well-marked occipital furrow. Postocular fixed cheeks wide, palpebral lobes situated well forward at about four-fifths length of glabella from posterior end. Preocular fixed cheeks narrow, outer margin parallel to margin of glabella. Posterior border furrows deep, shallowing abaxially.

Discussion. The cranidium differs from that of *P. vacuvertis* in having a narrower anterior width to the glabella, more even width (trans.) to the preocular fixed cheeks, and particularly in the considerably more forwardly placed palpebral lobes. Thus although the species is represented by only a single specimen it is clearly distinguishable from *P. vacuvertis*. It is, however, very similar to *P. rara* figured by Dean (1966, p. 133, pl. 1, figs. 1. 2. 7) from the Letna Formation (Caradoc) of Bohemia who remarked on the presence of faint glabellar furrows in one of Barrande's illustrations (Barrande 1852, pl. 29, fig. 21; see also Barrande 1872, pl. 5, fig. 27). The cranidium of *P.* n. sp. aff. *rara* (Henry 1980, p. 111, fig. 50; pl. 24, figs. 7, 9–11) from the Caradoc of Normandy is also very similar to the present material. Until a pygidium is known from Saudi Arabia we prefer to leave the nomenclature open.

Family DALMANITIDAE Vogdes, 1890
Subfamily ACASTINAE Delo, 1935
Genus KLOUCEKIA Delo, 1935

Type species. Phacops phillipsi Barrande, 1846.

Kloucekia sp.

Plate 47, fig. 2

Material. H60, H71. Internal moulds of cephalon.

Horizon. About 7 m below top of Hanadir Shale, associated with *Plaesiacomia vacuvertis* Thomas.

Description. Cephalon over half as long as wide, with rounded anterolateral margins, and slightly pointed anteriorly. Glabella reaches (?) anterior margin, sides converge as far back as basal furrows then run parallel. Axial furrows shallow. S1 short, directed inwards and slightly backwards, deep over most of length but shallow near axial furrow. L1 subrectangular in outline, but bulbous adaxially. S2 very faint, subparallel to S1, slightly curved forwards and not reaching axial furrow. S3 very faint, directed inwards and backwards at about 45° to axial furrow, barely discernible adaxially, terminating in shallow pit in axial furrow. Occipital ring delimited by deep occipital furrow behind L1. Median part of ring wider (sag.) where shallow occipital furrow is forwardly flexed. Eyes crescent-shaped in outline, running from just outside axial furrow behind shallow pit at end of S3 to level with extreme posterior part of L2. At least twenty-five vertical rows of eye lenses (preservation poor) showing hexagonal packing; up to six lenses per row. Anterior course of facial suture obscure; from eye it converges towards anterolateral margin of glabella. Behind eye, suture curves outwards and forwards, then backwards to lateral margin. Genal angles apparently rounded. Posterior border furrows wide, as deep as median part of occipital furrow, dying out at genal angles. Free cheek with faint border furrow. Cephalon with very low convexity longitudinally; transversely the lateral portions of the cephalon slope steeply outwards. Only ornament present is fine tuberculation on doublure.

Discussion. The deep S1, weak S2 terminating before the axial furrow, weak S3 and apparent absence of genal spines recall features seen in species of *Phacopidinia*, *Kloucekia*, and *Morgatia*. However, according to Hammann (1974, p. 96), *Morgatia* has large eyes reaching back to near the posterior border, bifurcating S1 at their inner ends, and S3 which join the axial furrows at right angles. None of these features is seen in the present specimen. With regard to the two former genera (see discussion in Henry 1980, pp. 123–127), the Arabian specimen does not show the typical outward curve of the axial furrow between S1 and S3, although in other characters the specimen has much in common with these two related genera. Dean (1961, p. 321) remarked that the only difference between the two genera is the mucronate pygidium of *Phacopidina*. Dr. J.-L. Henry, University of Rennes, kindly studied a photograph of specimen H71 (Pl. 47, fig. 2) and remarked that the apparent absence of a flat anterior border suggested that the specimen may be assigned to *Kloucekia* and in particular to *K. drevermanni drevermanni* (Hammann 1974, p. 80) from the Llanvirn of Spain. The Arabian specimens, although rather poorly preserved, differ from the Spanish species in having shorter (exsag.), more forwardly placed eyes and more inwardly directed S1 furrows. Until more material is available the specimens are provisionally referred to *Kloucekia* sp.

Family TRINUCLEIDAE Hawle and Corda, 1847
Subfamily HANCHUNGOLITHINAE Lu, 1963
Genus NINGKIANOLITHUS Lu, 1954

Type species. Cryptolithus welleri Endo, 1952.

Ningkianolithus hanadirensis sp. nov.

Text-fig. 3

Diagnosis. Ningkianolithus with radial rows of pits widely spaced and often irregular in front of glabella. Outer arcs of pits frontally and laterally only slightly larger than remainder. Up to six arcs of pits anterolaterally. Anterolateral margin of fringe geniculate, with short spine occasionally developed. Eye tubercle, eye ridge, and very faint genal caeca present. Genal spine in line with lateral margins of fringe.

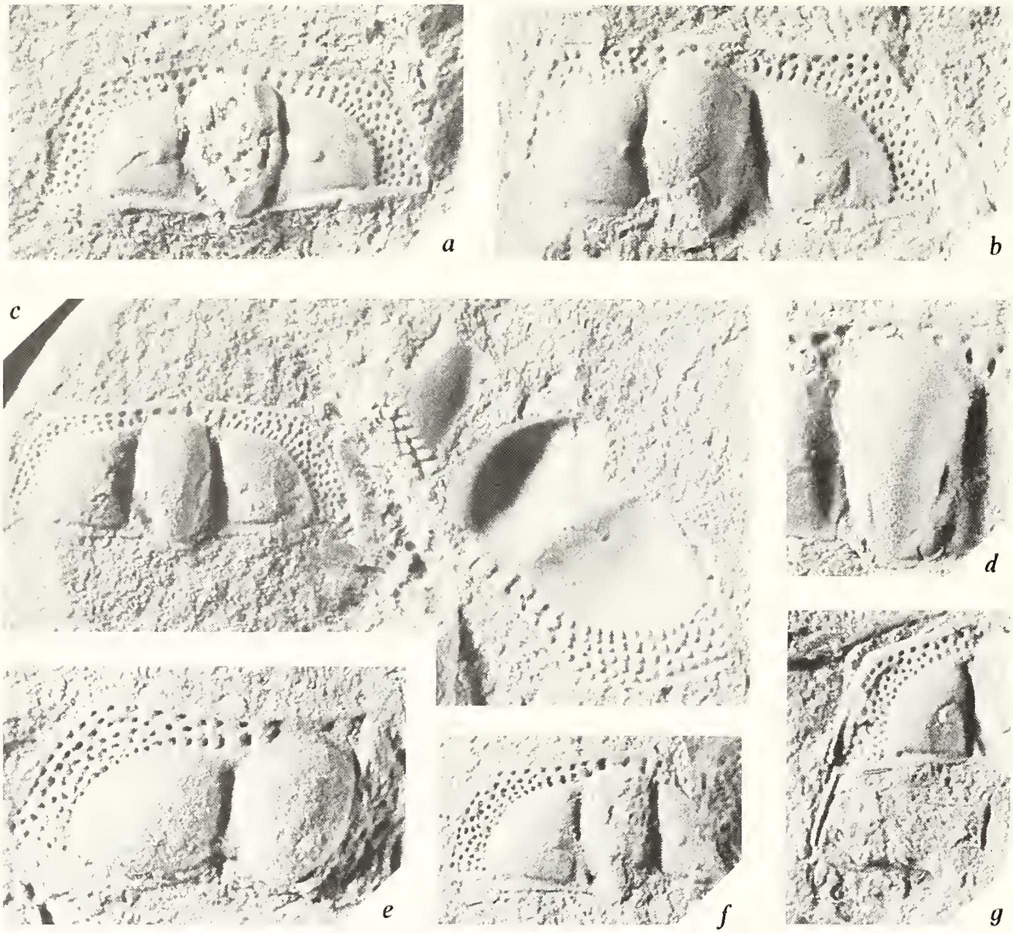
Type material. Holotype, It 18820, internal mould of cephalon. Paratypes, It 18821–18825. It 18821, 18823, 18824, 18825, internal moulds of cephalon; It 18822, external mould of cephalon. Four other specimens housed in the Geology Department, King Saud University, Riyadh, Saudi Arabia (H25, 77, 78, 79).

Horizon and locality. Base of Hanadir Member, Tabuk Formation, immediately above junction with Saq Formation. Al Hanadir (26° 27′ 50″ N., 43° 27′ 20″ E.), about 53 km west-north-west of Buraydah, Al Qasīm Province, Saudi Arabia.

Derivation of name. After locality known as Al Hanadir where the specimens were found.

Description. Cephalon just over twice as wide as long, excluding genal spines, and ranging in length from 3·25 to 5·5 mm. Anterior margin forwardly flexed in front of glabella, slightly curved for much of cephalic width, then directed backwards and outwards through sharp angle where very short anteriorly directed spines are situated. Glabella expands forward, anterior margin gently curved, preglabellar field absent. At least two pairs of faint glabellar furrows present in posterior half of glabella, weakly defined alae. Axial furrows shallow with faint anterior fossula. Glabella with quite strong traverse convexity, highest part of glabella just anterior to midlength. Occipital ring short (sag.) and backwardly curved; occipital furrow shallow medianly, with well-marked lateral occipital pits. Cheeks gently convex, steeply declined laterally. Prominent eye tubercle situated about two-fifths the length (exsag.) of the cheek from posterior border and slightly nearer to axial furrow. Thin eye ridge runs inwards and slightly forwards from eye tubercle to axial furrow. Very faint genal caeca extends from posterolateral side of eye tubercle, curves backwards between posterior fossula and fringe, and cuts posterior border. Posterior border furrow wide near glabella, narrowing distally to posterior fossula. Posterior border narrow (exsag.), convex. Faint reticulation on glabella and cheeks, present on internal and external moulds (text-fig. 3*d*).

Fringe more or less flat anteriorly, lateral portions sloping gently outwards. Fringe narrow in front of glabella (constricted by frontal lobe of glabella), widening evenly to angulation, then of even width to posterior border. Marginal border broad, upturned anteriorly, widest at angulation. Genal spines at least three-quarters as long as glabella, directed backwards and slightly outwards, forming more or less straight line with lateral margin of fringe. Girder submarginal(?) (text-fig. 3*g*) on lower lamella, no trace of terrace lines. In the specimen where the pits are most regularly arranged (text-fig. 3*e*) the notation is as follows: I_1: 1–18 (with auxiliary pits between R15–16), radius O not developed; I_2: 5–18 (auxiliary pits between R7–8); I_3: 7–15, then irregular; I_4: 8–?13 (including a few irregular auxiliary pits); I_5: 10–12; I_n: 1–17 (then unclear), with auxiliary pits between R7–11. Radial arrangement fairly good on outermost three arcs posterior to about R8, and on I_4, I_5, I_n. A faint list is present between I_1 and I_2 from about R7 to R17, but dies out before genal angle. Pits are generally absent



TEXT-FIG. 3. *Ningkianolithus hanadirensis* sp. nov. *a*, holotype, It 18820. *b–g*, paratypes. *b*. It 18823; *c*. It 18821–18822; *d*. H79, internal mould; *e*. It 18825; *f*. H78, internal mould; *g*. It 18824. All × 5.

immediately in front of glabella although rarely I_n persists as the only arc (text-fig. 3*a*, *c*). Minor variations occur in pit numbers and degree of radial arrangement but the range considered is intraspecific. Generally the largest pits occur anteriorly and in the outermost three arcs anterolaterally; the smallest pits are posterior to about R5 in the innermost two or three arcs.

Discussion. The Arabian species cannot be closely compared to any described trinucleid species, although on balance the material is most like the later meraspid stages of *N. welleri* (Lu 1964, p. 299, fig. 2). *N. hanadirensis* differs from *N. welleri* of comparable size (Lu 1975, pl. XXXVII, figs. 5, 9) in having less swollen and more angular anterolateral margins to the fringe, and not possessing the enlarged marrolithid-like pits. Also the genal spines are directed outwards at their proximal ends. *N. honghuayuanensis* Chang (1964, pl. 6, fig. 4) also differs from *N. hanadirensis* in possessing an outer arc of enlarged pits, rounded and swollen anterolateral margins, and numerous, randomly disposed small pits on the rest of the fringe. *N. sichuanensis* Lee (1978, pl. 109, figs. 1–3) and *N. tongziensis* Yin (Yin and Lee 1978, pl. 184, fig. 9) both possess a large number of irregularly arranged pits on the lateral portions of the fringe.

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